The American Midland Naturalist

Devoted to Natural History

Primarily that of the Prairie States

Founded by J. A. Nieuwland, C.S.C.

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Dates of Publication

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Errata Graviora

P. 49, line 2 from below, read:
"nom. nov."

P. 50, lines 20 and 21, read:
"*Blitum*, sect. *Ambrina* (Spach) Beck in Reichenb. Icon. xxiv:118, 1908."

P. 51, line 16 from below, read:
"ssp. RETUSUM (Juss.) Aellen etc."

P. 51, line 8 from below, read:
"ovato-lanceolata vel late lanceolata, etc."

P. 51, line 5 from below, read:
"f. ANGUSTATUM Aellen."

P. 52, line 7, read:
"var. ANTHELMINTICUM (L.) A. Gray, Man. ed. 2, 364. 1856."

P. 59, line 16, read:
"*Blitum hastatum* Rydb. .... not Phil."

P. 66, line 13, read:
"*Ch. Fremonti sensu* Murr etc."

P. 68, line 19, read:
"ssp. EU-ALBUM Ludwig, emend. Aellen.—"

P. 69, lines 16 and 17, read:
"var. STEVENSII Aellen in Fedde Rep. spec. nov. **26**:131. 1929.—"

P. 69, lines 22 and 23, read:
"var DACOTICUM Aellen in Fedde Rep. spec. nov. **26**:131. 1929.—"

P. 72, line 11, read:
"1913, as to name, not as to plant described."

P. 75, lines 7 and 8 from bottom, read:
"f. CYMOSUM Aellen in Fedde etc."

P. 75, lines 5 and 6 from bottom, read:
"f. SPICATIFORME Aellen, l.c."

P. 75, lines 3 and 4 from bottom, read:
f. GRIFFITHSII Aellen, l. c."

P. 102 and 105:
Transpose figures 13 and 15; legends remain.

P. 118, line 3, read:
"and the decrease in the number of sporangia *visible* at the node is typical. (1706 N1)."

P. 148, delete eighth line from bottom of page which reads:
"Middle and lower Coal- measures; Great Britain."

The American Midland Naturalist

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Centennial Issue

Dedication

AS the centenary year of the University of Notre Dame draws to a close, botanists are commemorating the 100th anniversary of the birth of the late Edward Lee Greene. The same pioneering spirit which inspired the founder of the University pervaded Professor Greene's whole life, whether as a missionary or as a botanist. Of the fruits of his labor his herbarium and library are now among the cherished possessions of the University.

The *American Midland Naturalist,* founded at the suggestion of Professor Greene, presents in his honor the following contributions to systematic botany by his associates, students and friends. With few exceptions, the other contributions by the editorial staff and members of the Department of Biology indicate the fields of biological science normally considered within the range of the journal's policy. Obviously they could neither be centered around a main thesis nor could they as a whole be limited to a highly specialized subject. Such restrictions would defeat the aim and hope of all serious biologists who are increasingly concerned with the integration of biological knowledge and not with its complete disruption to further special interests and minor fields. Biology, then, is at the crossroads, and the day may yet come when we

can speak of the "new biology" in the same way as the "new systematics" is now being envisaged.

The modern *naturalist* takes full cognizance of this development, as is amply reflected in the pages of recent volumes of the journal. Through its continued sponsorship of the *American Midland Naturalist* the University of Notre Dame is thus contributing materially to the advancement of biological knowledge. The Centennial Issue was prepared as a token in recognition of this service as a benefactor of science.

THEODOR JUST.

Edward Lee Greene the Individual

Willis Linn Jepson

In a little tea room off Kew Green sat two American botanists one August afternoon in the year 1930. They had come to England from the United States for the study of types and original material preserved in the Herbarium of the Royal Botanic Gardens at Kew—of all places in the world one of the most important and delightful for study. On this day, as on other days, they conformed to the national habits of the English when it came the sacred hour of tea, committed no sacrilege by continuous work, but put their microscopes aside and wandered across Kew Green to a place of wayside refreshment. Here as they sat idly talking over the steaming cups the name of Edward Lee Greene chanced into conversation. One of these botanists was from Washington, the other from California. The man from Washington bent his head over the tea cup and said reflectively: "Greene had one of the most delightful personalities that I have ever known—at any time, anywhere. He was wholly unique and individual. He loved to jest and I can so well remember his mannerisms. He would put his hand up his nose with the forefinger pointing upward, with a little grimace and say: "I have swallowed a canary!" Meaning that he had found a certain well-known West American botanist in error, as he viewed it, and had written a little note setting him right so that he might go forward by the right path ever after!

The man from Washington sipped his tea while the man from California intervened: "Greene's mannerisms were unquestionably very marked. Persons constantly came into the laboratory at Berkeley bringing a flowering plant or a branch of a tree or shrub for him to name. His sense of smell was extremely acute and discriminating and his first action was always to thrust the plant or branch to his nose. It was a characteristic mannerism."

The man from Washington laid down his tea spoon and went on: "His ways of doing things were always interesting; they showed his habits of exactness, precision and delicacy. A refinement distinguished his movements, there was always a refinement in his manner of doing things. Once I was invited to make one of a company dining with him at his table. He took the carving knife and fork and in an instant, though not hurriedly, cut through the shoulder of lamb and served us with a mastery, a surety, a nicety that to me was the last word in elegance in carving meat portions. Then and there I resolved that when it came my time to serve at table, I meant to rise to that standard.

"Greene had a great capacity for and delighted in aphorisms. He loved to startle or surprise you by making some pithy and inclusive statement. If I were working on ferns he might, at the end of the day come down to my table and refer to my pile of ferns as "rubbish," as of no value. Grasses and ferns

he refused to be interested in or to regard them as of any especial value, botanically speaking.

"He must have been, I think, a very lonely man. The circumstances of his life served to bring this about. He was given to solitary botanizing. One day we chanced upon him in the woods near Cabin John up the Potomac River above Washington and invited him to go with us to our camp. He accepted and we rowed across the Potomac in a canoe. In our camp cabin we had a large chair over which was thrown a great deep red blanket. He sat in this chair. With his pink baby-like complexion, his head of cotton-white hair, his handsome features and fine frame, it was as if a prelate of the church were sitting on his throne. Possibly it might have been better if Greene had spent his life as a real recluse. He was a monk by spirit, by temperament, by predisposition. His loneliness was perhaps much accentuated by his shyness. Greene was shy, although few persons, who knew him only casually, might ever guess it."

Then the man from Washington paused and for a moment gave his attention to the second jug of tea brought by the waitress. The man from California filled in during this pause: "It is my remembrance of an incident at Berkeley," he said, "that confirms this comment of yours on his shyness. One winter day he and I were in the Garden of Native Plants, lying in the hollow below Old North Hall, planting seed. As we returned after our task to South Hall where the Department of Botany had its quarters, we chanced into a great concourse of students on the walk, just let loose from a lecture room at the end of the hour. Greene said, 'Oh, look at this we have to meet! What shall we do!' in a way that indicated his shyness at thus facing unexpectedly a crowd. However, he had no shyness with his students when in the laboratory or herbarium nor when in the lecture room."

The man from Washington took up again the thread of reminiscence: "Greene's personality was also revealed in what he said and wrote. In his use of words he was most select, and what he said would bear publication as well or better than that which most of us laboriously write. His letters are fine examples of elegant and felicitous expression, and could in every case be printed as they stand."

"There is in the possession of the Smithsonian Institution the manuscript of the second volume of Greene's Landmark's of Botanical History. There are a few lacunae; it was not left in perfect condition but the gaps could readily be filled in by a man like Professor H. H. Bartlett, since Bartlett is one who was personally in thorough sympathy with Greene."

"The publication of the second volume of the "Landmarks" is not provided for by any present arrangements. There is no money at present for it; the manuscript is not ready. It will be published whenever the Smithsonian Institution is called upon to do it, whenever some interest exerts itself to that end. The treatise, of course, represents Greene's particular view of the history of

botanical events. The view is colored by all that he stands for, because he is here, as always, a partisan."

There was the clink of shillings on the tea-table and the two men rose, crossed Richmond road and walked past Saint Anne's Church across Kew Green to the Herbarium. The man from Washington was Dr. William Ralph Maxon, Curator of the United States National Herbarium, the other was myself. And so I queried Dr. Maxon: "Will you not write out what you have just said, it is so felicitous, so happy, that it may well be printed in Erythea or elsewhere as a picture of Greene's personality." To this after a bit of hesitation, Dr. Maxon made a polite assent.

On reaching my own work alcove in the Herbarium the reflection crossed my mind that the hours of my friend at Kew were too brief, those at Washington too constantly overwhelmed by a multitude of duties to expect that he would ever find time to record such a reminiscence. A power I have is this: listening to a discourse which has interest, I can within one hour or two hours afterwards write it out quite perfectly. On this occasion I did so and there is now preserved a picture of Greene's personality, judicial and unprejudiced, and divested of immaterial matters. It is my hope that it will help preserve the memory of a man who was every inch an individual.

UNIVERSITY OF CALIFORNIA,
BERKELEY, CALIFORNIA.

Sertulum Greeneanum

John Thomas Howell

Introduction

In the spring and summer of 1942, while I was intensively studying the species of *Phacelia* related to *Phacelia humilis* T. & G., it became increasingly evident that a final revision of the group could not be prepared until the identity of *Phacelia inconspicua* Greene was established. Hence, in October, I visited the Greene Herbarium at the University of Notre Dame, and there I was not only able to study the type of *Phacelia inconspicua* and to examine all of Greene's rich and critical collection in *Phacelia*, but I was also able to clear up the identity of a number of western plants, particularly in the genus *Cirsium*. To Dr. Theodor Just and his colleagues, I am grateful for their attentiveness which made my visit most profitable and enjoyable.

It was partly from respect and partly from sentiment that one memorable afternoon I visited the small cemetery in a secluded part of the campus where Edward Lee Greene is buried. The simple monument of granite carried only his name and the dates 1843—1915. As Dr. Just and I returned through the colorful autumnal woods towards that magnificent monument to his life work, his herbarium and library, we discussed the possibility of a series of papers in systematic botany which might memorialize in 1943 the centennial of his birth. It is with deep respect that I offer the following three-parted *sertulum* in honor of one of America's keenest and most brilliant botanical personalities.

I. A Systematic Study of Phacelia humilis and its Relatives

Phacelia humilis and its immediate relatives are those annual species of the subgenus *Euphacelia* in western North America in which the leaves or primary leaf-divisions are entire. There are nine species in the group and all of them except *P. inconspicua* Greene occur in California where six of them are endemic.

The group has not been well understood. I first attempted a key to the species early in the spring of 1930, but the historical concept of *P. humilis* had been so confused by Brand (Das Pflanzenr. IV. 251), I made no progress at that time. During the last decade, extended field work through northern and eastern California and the accumulation of herbarium specimens of the different species have clarified most of the entities involved; and more recently I have had the privilege of examining extensive collections in many institutions. Besides the specimens in the California Academy of Sciences (CAS) where most of the studies have been made, I have seen the collections from the following institutions:

Dudley Herbarium, Stanford University (DS)
Field Museum (F)
Frank Peirson (FP)
Gray Herbarium, Harvard University (G)
Intermountain Herbarium, Utah State Agricultural College (IU)
Missouri Botanical Garden (M)
University of Nevada (N)
Greene Herbarium, University of Notre Dame (ND)
New York Botanical Garden (NY)
Pomona College (P)
Rancho Santa Ana Botanic Garden (RSA)
University of California (UC)
United States National Herbarium (US)
Willamette University (W)
Washington State College (WS)

To the curators of these collections, I am very grateful for the privilege of studying the material. The abbreviations in parentheses are used in the customary manner in the citation of specimens in the following systematic treatment.

KEY TO THE SPECIES

1. Filaments long-hairy ..... 1. *P. humilis*
1. Filaments smooth or tuberculate, not long-hairy.
2. Capsule distinctly compressed along sutures; plants not glandular; corolla mostly 5-6 mm. long ..... 2. *P. Breweri*
2. Capsule rounded at sutures; upper stems and inflorescences glandular-hairy (except in *P. inconspicua*); corolla 5 mm. long or less (except in *P. Greenei*).
3. Corolla 2.5-5 mm. long, tubular-campanulate to open-campanulate, not rotate.
4. Stem usually not markedly elongate below the first foliage leaves, hirsutulous.
5. Corolla promptly deciduous.
6. Upper stems and inflorescence not glandular; corolla tubular. ..... 3. *P. inconspicua*
6. Upper stems and inflorescence glandular; corolla open-campanulate.
7. Styles divided 1/2-2/3 length; fruiting calyx-lobes usually markedly unequal. ..... 4. *P. austromontana*
7. Styles divided nearly to base; fruiting calyx-lobes nearly equal. ..... 5. *P. Eisenii*
5. Corolla marcescent or tardily deciduous, campanulate at first, becoming tubular-contracted after anthesis.
8. Leaves ovate to oblong-elliptical; capsule elliptical; seeds ovate-lanceolate, apex sharply acute ..... 6. *P. marcescens*
8. Leaves oblong-linear; capsule subglobose; seeds plumply ovate, obtuse ..... 7. *P. Quickii*
4. Stem below first foliage leaves markedly elongate and usually more than half the height of the plant, glabrous and glaucous ..... 8. *P. racemosa*
3. Corolla 5-6 mm. long, rotate-campanulate ..... 9. *P. Greenei*

1. PHACELIA HUMILIS T. & G., Pac. R.R. Surv. 2:122, pl. 7. 1855.

Annual, stems simple and erect or the branches widely spreading from the base, 0.5-2 dm. tall, thinly or densely clothed with hirsute and hirsutulous hairs, scarcely at all glandular; leaves with 1 or 2 pairs opposite at base, alternate above, linear-oblong or elliptical to ovate, 1-4(-10) cm. long, 0.3-2 cm. wide, hirsutulous or the hairs subappressed, margin always entire, apex acute, cuneate at base, petioles of lower leaves to 2 cm. long, more or less bordered, the uppermost bract-like leaves nearly sessile; racemes solitary or in 2's or 3's, flowers rather distant below, crowded above, pedicels 1-3 mm. long;

calyx-lobes in flower linear to narrowly oblong, 2.5-3.5(-6) mm. long, 0.3-0.6 mm. wide, obtusish, in fruit 5-7(-12) mm. long, 0.3-0.75(-1) mm. wide, hirsute, the lobes nearly equal in size; corolla open-campanulate, violet, 4.5-5(-7) mm. long, the lobes about 2-3 mm. long; corolla-scales quadrate, 1-1.5(-2) mm. long, united a little to base of filaments, the edges of adjacent pairs connivent, the pair only about 0.5 mm. wide; stamens scarcely exserted to long-exserted, 4-5.5(-8.5) mm. long, the filaments with a few long hairs near the middle, anthers about 0.5 mm. long; style including branches 4-7(-11) mm. long, the branches 2-5.5 mm. long, the style sparsely hirsutulous to the branches; ovary about 1 mm. long, long-hirsute, ovules 4; capsule narrowly to plumply ovate, 2.5-3.5(-4) mm. long, acute below short apiculation, sparsely hirsute and rather evenly and densely puberulous; seeds 2-4, narrowly ovatish, 1.5-3 mm. long, brown, rather finely pitted.

Sagebrush flats to forested meadow-borders from central Washington south to western Nevada and eastern California.

As might be expected in a species ranging so far and growing under such diverse habitats as Basin flats and subalpine uplands, *P. humilis* varies considerably in appearance and in size of parts, but only in the southern part of its range in California does a variety worthy of nomenclatural recognition stand out. Plants from the Tehachapi Mts. in Kern County and selected specimens from Mono County have flowering and fruiting parts as much as twice as large as in typical plants. The two species proposed by Brand which are here reduced to synonymy, do not differ sufficiently from the typical form of the species to be recognized even varietally. Undoubtedly Brand confused *P. humilis* with its relatives, *P. Quickii* and *P. austromontana*, when he described his two species.

KEYS TO VARIETIES OF PHACELIA HUMILIS

Stamens little-exserted from corolla, usually 4-6 mm. long; fruiting calyx 5-8 mm. long; seeds 1.5-2.5 mm. long. ..... 1a. var. *typica*

Stamens conspicuously exserted from corolla, 6-8 mm. long; fruiting calyx 8-12 mm. long; seeds 2.5-3 mm. long. ..... 1b. var. *Dudleyi*

1a. **P. humilis** T. & G. var. **typica** J. T. Howell, nom. nov.

P. humilis T. & G., loc. cit. *P. irritans* Brand, Beilage, Jahresb. Kgl. Gymnas. Sorau, 7 (1911). *P. violacea* Brand *in* Fedde Repert. spec. nov. **17**:319 (1921).

Inflorescence thinly or densely hirsutulous or more rarely hirsute, rarely minutely glandular, flowers generally distant below and more crowded above, pedicels 1-3 mm. long; calyx-segments in flower 2.5-3.5 mm. long, in fruit linear to narrowly oblong, 5-7 mm. long, 0.3-0.75 mm. wide; corolla mostly 4.5-5 mm. long; stamens 4.5-5.5 mm. long; style and branches 4-7.5 mm. long; capsule 2.5-3.5 mm. long; seeds narrowly ovatish, 1.5-2.5 mm. long.

Representative collections: WASHINGTON: Buck Mt. road about 2.5 miles from Twisp cut-off, Okanogan Co., *Fiker No. 2458* (WS); near Egbert Spring, Douglas Co., *Sandberg & Leiberg No. 350* (lectotype of *P. violacea* Brand, the first-cited collec-

tion; CAS, F, G, M, NY, UC, US); Horse Lake west of Wenatchee, Chelan Co., *Whited No. 1103* (G, M, US, WS); Yakima region, Yakima Co., *Brandegee in 1883* (G, M, UC).

OREGON: Willow Creek Canyon, Harney Co., *Peck No. 19006* (W); Steens Mts., Harney Co., *Peck No. 14051* (F,W); Malheur Co. (Peck Man. Higher Plants Oregon, p. 590).

NEVADA: Havallah Mts. (Sonoma Range), *Watson No. 872* (G, NY, US); Santa Rosa Mts., Humboldt Co., *Cusick No. 2132* (F, G, M, ND, UC, US, WS), *Train No. 265* (N, NY); West Humboldt Mts., Pershing Co., *Greene in 1894* (ND, NY); Third Creek near Mt. Rose, Washoe Co., *J. T. Howell No. 14101* (CAS, F, IU, M, ND); Glenbrook, Douglas Co., *L. S. Rose No. 421* (CAS); Kings Canyon, Ormsby Co., *C. F. Baker No. 921* (CAS, G, M, ND, NY, P, UC, US).

CALIFORNIA: "Sierra Nevada Mountains," *Lieut. Beckwith No. 41* (G, type, NY); Fandango Pass, Warner Mts., Modoc Co., *J. T. Howell No. 12062* (CAS, DS, F, FP, G, IU, NY, P, US, UC); Parker Creek, 6000 ft., Warner Mts., Modoc Co., *Payne No. 613* (CAS); Grasshopper Valley, Lassen Co., *Eastwood & Howell No. 8324* (CAS); Horse Lake, Lassen Co., *J. T. Howell No. 11891* (CAS, F); Chilcott, Plumas Co., *Eastwood No. 14878* (CAS); Red Clover Valley, Plumas Co., *Heller & Kennedy No. 8738* (CAS, DS, F, G, M, NY, US); Little Truckee River, 6,300 ft., Sierra Co., *Hall & Babcock No. 4523* (type of *P. irritans* Brand, UC); Donner Lake, Nevada Co., *Heller No. 6866* (CAS, DS, F, G, M, NY, P, UC, US); Deer Park, Placer Co., *Walker No. 2030* (CAS, DS, F, G, M, NY, P, UC, US); Red Lake, Alpine Co., *Peirson No. 11614* (CAS, FP); Ebbets Pass, Alpine Co., *Eastwood & Howell No. 8494* (CAS); Twin Lakes Basin, Mono Co., *Peirson No. 10371* (CAS, FP); Buttermilk country, Inyo Co., *Duran No. 3470* (CAS, DS, F, G, IU, M, NY, P, RSA, UC, US, WS); near Lake Sabrina, Inyo Co., *Davidson No. 2921* (DS).

A collection of *P. humilis* said to have been made at Price, Carbon Co., Utah, June 12, 1900, (*Stokes*, DS, NY, UC, US), was undoubtedly made in middle western Nevada. Another *Phacelia, P. demissa* Gray, the distribution of which centers in eastern Utah, has been mistakenly reported from "Wadsworth, Nevada," on the basis of a specimen reputedly collected there by Miss Stokes on June 12, 1900 (UC; cf. Brand, Das Pflanzenr. IV. 251: 119).

Out of more than eighty collections of *P. humilis* that have been examined, two have been noted with glabrous filaments: alpine summit of Chumstick Mt., Chelan Co., Washington, *Thompson No. 8489* (DS, NY); Sierraville, Sierra Co., California, *Ripley & Barneby No. 4533* (CAS). Since the plants of both these collections are very young, the absence of hairs on the filaments is regarded as a seasonal abnormality worthy of note but not of taxonomic import.

1b. **P. humilis** T. & G. var. **Dudleyi** J. T. Howell, var. nov.

Inflorescentia hirsuta et paulum glandulosa, densiflora, pedicellis circa 1 mm. longis; lobis calycis ad anthesin 4-6 mm. longis, in fructu valde accrescentibus, linearibus, 8-12 mm. longis et 0.5-1 mm. latis; corolla campanulata usque ad 7 mm. longa; staminibus 6-8 mm. longis, exsertis, filamentis sparse et longe pilosis; stylo et ramis usque ad 11 mm. longis; capsula turgide ovoidea, 4 mm. longa; seminibus elliptico-ovatis, 2.5-3 mm. longis.

Type: No. 8313, Dudley Herbarium, Stanford University, collected in the vicinity of Bisses Station, Tehachapi Mts., Kern Co., California, June 27, 1895, by W. R. Dudley, *No. 388*. Duplicate in Herb. Univ. Calif. Other collections from the Tehachapi Mts. are: *Davidson in 1907* (DS), *Hasse &*

Davidson No. 1711, June, 1907 (US); Water Canyon, *Abrams & McGregor No. 433* (P, US in part).

Occasionally on the east side of the central Sierra Nevada extra robust specimens of *P. humilis* have been collected in which the sizes of the flowers and fruits approach or equal the sizes given for the Tehachapi plants. Representative of this variant are the following specimens from Mono County: Fales Hot Springs, *Winblad in 1938* (CAS); Long Valley, *Noldeke in 1938* (CAS), *J. T. Howell No. 14304* (CAS, G, US); Mammoth, *Duran No. 1948* (CAS).

2. PHACELIA BREWERI Gray, Proc. Amer. Acad. 10:317. 1875.

Root annual; stems simple at base and branching above or much-branched near the base, substrictly erect or the branches widely spreading and somewhat flexuous, 0.5-3 dm. long, hirsute and puberulent, not obviously glandular; leaves opposite at base, alternate above, lanceolate to ovate-elliptic, 1-4 cm. long, 0.3-2 cm. wide, entire or the lower generally pinnately parted with one to several lobes, the lobes sometimes nearly discreet, the veins impressed above and raised below, subappressed-hirsutulous or strigose, acute at apex, cuneate at base, petiole more or less bordered, to 3 cm. long below, almost none above; racemes in 2's or 3's at the ends of branches, becoming elongate and to 12 cm. long, the lowest flowers distant, crowded above, pedicels 1-2 mm. long; calyx-segments in flower about 3 mm. long, 0.3-0.5 mm. wide, oblong-linear, in fruit 4.5-5 mm. long, about 0.5 mm. wide, linear, nearly equal, hirsute and puberulent, not glandular; corolla light blue, open-campanulate, 5-6 mm. long, tube 3 mm. long; corolla-scales semi-lanceolate to semi-ovate, 1.5 mm. long, adjacent pairs free or united by their free edges, attached a little to the base of the filaments; stamens included or one or more exserted a little, 4-4.5 mm. long, filaments glabrous, anthers about 0.5 mm. long; style including branches 3 mm. long, the branches 1.3-2 mm. long, the style and the lower part of the branches hirsutulous; ovary about 1 mm. long, hirsute, ovules 4; capsule broadly ovate, 3 mm. long, 2.5 mm. wide, strongly compressed especially along sutures; seeds 1 or usually 2, ovate-lanceolate, 2-2.25 mm. long, acutish, brown, finely pitted.

Inner South Coast Ranges from Contra Costa County south to Fresno and San Benito counties, California, on open or brushy slopes in clay or rocky soil, 260 to 4500 ft.

Representative specimens: all from CALIFORNIA: Mt. Diablo, Contra Costa Co., *Brewer No. 1058* (G, type; UC), *Hall & Essig No. 10140* (CAS, DS, F, G, M, NY, P, UC, US); Arroyo Mocho, Alameda Co., *Elmer No. 4433* (CAS, DS, M, NY, P, UC, US), *J. T. Howell No. 864* (CAS); Mt. Hamilton, Santa Clara Co., *C. F. Baker No. 637* (CAS, G, M, NY, P, UC, US, WS), *Eastwood & Howell No. 9684* (CAS); Madrone Springs, Santa Clara Co., *Eastwood & Howell No. 4590* (CAS, F); Hospital Canyon, San Joaquin Co., *J. T. Howell No. 13763* (CAS); Arroyo del Puerto, Stanislaus Co., *C. W. & H. K. Sharsmith No. 1539* (CAS); Los Baños Creek, Merced Co., *Short No. 49* (UC); west of Panoche, San Benito Co., *Eastwood & Howell No. 4264* (CAS, M); Hernandez, San Benito Co., *Dudley in 1899* (DS);

"Cholame Valley, Monterey Co.," May, 1878, *Lemmon No. 3079* (G); Mercy Hot Springs, Fresno Co., *Eastwood & Howell No. 5117* (CAS).

The last-cited specimen is noteworthy because in it all the leaves are entire. At least some leaves in most of the other collections that have been examined are pinnately lobed.

3. PHACELIA INCONSPICUA Greene, Erythea 3:24. 1895.

Root annual; stems erect, branching from the base, 0.7-1.5 dm. tall, hirsute and hirsutulous with longer and shorter non-glandular hairs; leaves elliptical, to 3.5 cm. long and 1.2 cm. wide, entire, green above and paler below, hirsute and hirsutulous with spreading non-glandular hairs, apex acute, at base cuneate and drawn down along a short winged petiole; racemes shorter than, and somewhat concealed by, the leaves, becoming elongate and 7 cm. long or the flowers subcapitate-congested at the ends of the upper branchlets, the lowest flowers in the racemes distant, congested above, pedicels 1-3 mm. long; calyx-segments in flower about 3 mm. long, in fruit becoming 5-7 mm. long, to 1 mm. wide, linear-oblong to linear-oblanceolate, about equal in length, a little unequal in width, hirsute and hirsutulous, not glandular; corolla apparently whitish ("or with a very dull bluish tinge" acc. Greene), 3 mm. long, tubular-campanulate, the lobes erect, not spreading, rounded, entire, a little more than 1 mm. long; corolla-scales about 1 mm. long, narrow, generally semi-lanceolate but a little irregular and drawn upward as a narrow line, the edges of adjacent scales distinct; stamens equalling or barely exceeding the corolla, 2.5 mm. long, the filaments smooth and glabrous, anthers 0.3 mm. long; style and branches about 2.5 cm. long, the branches about 1 mm. long, the style more or less hairy up to the branches; capsule roundish-ovate, 3 mm. long, 2 mm. wide, gradually narrowed to a short beak, pubescent and a little hirsutulous above, seeds 4.

This very distinct and critical phacelia is known only from the type collection made by E. L. Greene in the West Humboldt Mts., Pershing Co., Nevada, on July 18, 1894 (ND). In morphological characters it is intermediate between *P. humilis* and *P. austromontana*, and it may well represent the modern and relictual form from which originated *P. austromontana* and its relatives.

4. PHACELIA AUSTROMONTANA J. T. Howell, Leafl. West. Bot. 3:190. 1942.

P. humilis T. & G. var. *lobata* Davidson, Bull. S. Calif. Acad. Sci. 5: 61 (1906).
P. lobata (Davidson) Jepson, Fl. Calif. 3:253 (1943).

Root annual; stems simple below and few-branched above and substrictly erect, or usually rather widely and fastigiately branched from the base, 0.5-2 dm. tall, hirsute-glandular with longer and shorter nonglandular hairs and few or many capitate glands; leaves opposite below (1 or 2 pairs), alternate above, entire, saliently few-toothed or pinnately lobed with 1 to 4 lobes on each side, generally 1-3 cm. long and 0.2-1.5 (or 2) cm. wide, linear-lanceolate to oblong or ovatish, hirsute and glandular, veins impressed above and raised

below, apex acute, base cuneate, petiole to 2 cm. long; racemes loosely or densely flowered, little exceeding the leafy part of the plant but becoming elongate in age and up to 5 cm. long, pedicels 2-3 mm. long below, shorter above, or rarely about 1 cm. long, the pedicels of the lowest flowers spreading or recurved in fruit; calyx-lobes unequal in length and width, in flower 2.5-3.5 mm. long, 0.25-1 mm. wide, linear to oblanceolate, in fruit hirsute and more or less glandular, 3.5-5.5 (or 8) mm. long, 0.3-1.5 (or 2) mm. wide, linear to spatulate-oblanceolate, subacute; corolla lavender or pale blue, promptly deciduous, open-campanulate, 3-5 mm. long, the tube 2-2.5 mm. long; corolla-scales rectangular, 0.75-1 mm. long, the free edges of adjacent pairs connate; stamens about equalling the corolla or a little longer, 2-4 mm. long, the filaments glabrous, smooth or with retrorse tuberculate processes, anthers 0.3-0.5 mm. long; style and branches 3-4 mm. long, style hairy near the base, the branches 1.25-2 mm. long; ovary about 1 mm. long, the upper part long-hairy, ovules 4; capsule plumply ovate, 3-3.5 mm. long, rather prominently beaked, non-glandular hairs pilose and puberulent, capitate glands few; seeds 2-4, 1.5-1.75 mm. long, oblongish or oblong-ovate, subacute, light brown, coarsely pitted.

Loose sandy or rocky soil of mountain slopes, chiefly in ranges bordering the Mohave Desert, California, from the Sierra Nevada and Panamint Range in Tulare and Inyo counties southward to the San Jacinto Mts., Riverside County, 6000 to 9000 ft.; locally in the Pine Valley Mts., Washington County, Utah.

Representative collections: CALIFORNIA: "North Middle Tule," Tulare Co., *Purpus No. 3080* in part (UC); Erskin Creek, Kern Co., *Purpus No. 5292* (G, M, UC, US); Mt. Pinos, Ventura Co., *J. T. Howell No. 3841* (CAS, F, G, IU, M, ND, NY, US); Topatopa Mts., Ventura Co., *Abrams & McGregor No. 74* (DS, US); South Fork Rock Creek, 6000 ft., San Gabriel Mts., Los Angeles Co., *Peirson No. 7940* (CAS, type; FP); Lowell Mine, Big Rock Creek, Los Angeles Co., *Hasse & Davidson No. 1491* (Herb. Los Angeles County Museum, type of *P. humilis* var. *lobata* Dav., a mixture of *P. austromontana* and *P. Davidsonii* Gray); San Antonio Canyon, 7500 ft., San Bernardino Co., *Peirson in 1927* (CAS, FP); Sugarloaf (Mt. San Bernardino), San Bernardino Mts., San Bernardino Co., *J. & H. W. Grinnell in 1906* (CAS, US), *Peirson No. 8986* (CAS, FP, P); Bluff Lake Trail, 7700 ft., San Bernardino Mts., San Bernardino Co., *Hilend No. 523* (CAS); Chino Canyon, 8200 ft., San Jacinto Mts., Riverside Co., *Jaeger No. 569* (US); Surprise Canyon at 7700 ft. and 9500 ft., Panamint Mts., Inyo Co., *J. T. Howell in 1928* (CAS); trail from Wild Rose Canyon to Telescope Peak, 8800 ft., Panamint Mts., *Munz No. 14791* (CAS, P).

UTAH: Oak Grove Camp above Leeds, Pine Valley Mts., Washington Co., *Cottam No. 8831* (CAS, UC), *Ripley & Barneby No. 4936* (CAS, F, G).

5. PHACELIA EISENII T. S. Brandg., Zoë 2:252. 1891.

Root annual; stems slender and flexuous, simple below or few- to many-branched from the base, erect or widely spreading, 0.2-1.5 dm. tall, hirtellous to hirsutulous with non-glandular hairs and with a few capitate-glandular hairs intermixed; lower leaves more or less rosulate-clustered or the leaves distant and the first one or two pairs above the cotyledons opposite, the upper leaves alternate, leaves simple or pinnately parted with 1-3 pairs of

small lobes below the larger terminal lobe, oblong to elliptic, 0.5-2 cm. long, 0.2-1 cm. wide, hirsutulous and a little glandular, acute or rarely subobtuse, cuneate, petioles to 2 cm. long, usually much shorter; racemes usually slender and elongate with scattered flowers, pedicels 1-7 mm. long or even to 15 mm. long in lax shade forms, the longer lower pedicels spreading or recurved; calyx-segments in flower about equal, 1.5-2.3 mm. long, 0.25-0.5 mm. wide, in fruit 3-5 mm. long, 0.25-0.6 mm. wide, linear or linear-spatulate, hirsutulous and a little glandular; corolla lavender, campanulate to subrotate-campanulate, 2-4 mm. long, tube 1-2 mm. long; corolla-scales small, distinct, semi-lanceolate to semi-ovate, 0.3-0.75 mm. long; stamens included, 1.5-3 mm. long, filaments smooth or with few retrorse processes, anthers 0.2-0.5 mm. long; style parted nearly to the base, 1-4 mm. long, glabrous or the lower part hirtellous and glandular, the undivided part about 0.2 mm. long, persisting as an apiculation on the capsule; ovary about 0.5 mm. long, ovules 4; capsule 2-3 mm. long, ovate to subglobose, subacute, hirtellous, glandular hairs present or lacking; seeds 1.5 mm. long, elliptical or oblongish, ends obtuse, rather coarsely pitted, light brown.

Occasional in the middle and southern Sierra Nevada, chiefly on the western slope in the main forest belt from 4000 to 11000 feet, from Eldorado County south to Inyo and Tulare counties, California.

As a species, *P. Eisenii* is one of the most clearly marked, differing from all other species in the *P. humilis* relationship by its style parted almost or quite to the base. In habit, leaves, and size of flowers, however, it is rather variable, and although the variations are more or less correlated with the distribution of the species, they are not entirely clear-cut and there are puzzling intermediates. In general, it may be stated that in the north the leaves are entire and the corollas are smaller, while to the south, the leaves are frequently lobed and the corollas are larger. Several specimens from Fresno County, including the type of the species, are intermediate between the two: the leaves are occasionally lobed but the corollas are small like those in the northern variant. Based on size of flowers, two variants may be properly distinguished.

KEY TO VARIETIES OF PHACELIA EISENII

Corolla 2-3 mm. long; style 1-2 mm. long; leaves usually entire, rarely lobed ..... var. *typica*

Corolla 3.5-4 mm. long; style 2-4 mm. long; lower leaves usually lobed ..... var. *Brandegeana*

5a. **P. Eisenii** T. S. Brandg. var. **typica** J. T. Howell, nom. nov.

P. Eisenii T. S. Brandg., loc. cit., in part. *P. minima* Macbr., Contrib. Gray Herb. n. ser. **49**:38 (1917).

Leaves entire or rarely with one or several lobes; sepals in flower less than 2 mm. long; corolla campanulate or open-campanulate, 2-3 mm. long; stamens 1.5-2 mm. long; style 1-2 mm. long.

Phacelia minima Macbr. represents only a shade-form of *P. Eisenii* with

very lax habit and elongate pedicels. Specimens examined from the Gray Herbarium indicate that Macbride did not properly understand *P. Eisenii* and that he mistook *P. Quickii* for that species.

Representative specimens: all from CALIFORNIA: Echo Lake, Eldorado Co., *Randall in 1930* (UC); cliffs above Angora Lake, Eldorado Co., *M. S. Baker in 1904* (P); Jack Main Canyon, Tuolumne Co., *Sharsmith No. 3695* (CAS, WS); Lake Tenaya, Mariposa Co., *Congdon in 1890* (G, type of *P. minima* Macbr.), *Eastwood No. 463* (CAS); Vernal Falls, Yosemite Valley, Mariposa Co., *Chandler & Babcock No. 1037* (CAS, DS, F, M, P, UC, US), *J. T. Howell No. 16242* (CAS); Shadow Creek below Lake Ediza, Madera Co., *J. T. Howell No. 16800* (CAS); Fresno Co., *Eisen* (CAS, type); Bald Mt., Fresno Co., *Hall & Chandler No. 378* (DS, M, NY, UC, US); Harrison Pass Trail at 11000 ft., Tulare Co., *J. T. Howell No. 15805* (CAS); between Pinto Lake and Black Rock Pass, Tulare Co., *J. T. Howell No. 17345* (CAS, G); between Big Arroyo and Chagoopa Plateau, Tulare Co., *J. T. Howell No. 17434* (CAS, F); Bishop Creek, Inyo Co., *A. Davidson No. 2642* (DS).

5b. **P. Eisenii** T. S. Brandg. var. **Brandegeana** J. T. Howell, var. nov.

P. Eisenii T. S. Brandg., loc. cit., in part.

Foliis basalibus et inferioribus caulinis saepe pinnato-lobatis; sepalis ad anthesin 2-2.3 mm. longis; corolla subrotato-campanulata, 3.5-4 mm. longa; staminibus 3 mm. longis; ramis styli 2-4 mm. longis.

Type: No. 124970, Herb. Univ. Calif., collected by T. S. Brandegee at Frazer's Mill above Porterville, Tulare County, California. Other collections, all from Tulare County: Morro Rock, *Holman in 1933* (UC); Middle Tule River, 7000-8000 ft., *Purpus No. 1791* (UC); Dennison's Trail near Mountain Lake, 9500 ft., *Dudley No. 930* (DS; flowers large but leaves all entire).

6. PHACELIA MARCESCENS Eastwood ex Macbride, Contrib. Gray Herb. n. ser., 49:39. 1917.

Root annual; stems erect, simple below and few-branched above or with numerous branches from the base, 0.5-2 dm. tall, glandular-hirsutulous and more or less mephitic, the non-glandular hairs long and hirsute as well as short and hirsutulous, the glandular hairs black and capitate; leaves narrowly elliptical to ovate, generally 1-3.5 cm. long and 0.4-2 cm. wide, strigose above, hirsutulous below, more glandular below than above, the veins somewhat impressed above and raised below, margin entire or saliently lobed on the larger leaves, acutish at apex, narrowly to broadly cuneate at base, petiole to 3 cm. long, the uppermost reduced leaves nearly sessile; racemes densely flowered, generally becoming elongate and to 1 dm. long, mostly in 2's or 3's at the ends of branches, pedicels 1 mm. long; calyx-segments in flower only a little unequal, 2 mm. long, 0.25-0.5 mm. wide, in fruit 3-3.5 mm. long, 0.5-1 mm. wide, linear to oblanceolate, obtuse, somewhat hirsutulous and glandular; corolla marcescent, violet, open-campanulate at first becoming tubular after anthesis, 4 mm. long, the tube 2 mm. long, the lobes crenulate; corolla-scales 1 mm. long, the free edges of adjacent pairs connivent, the pair only about 0.3 mm. across, attached to base of filaments; stamens exserted, 5.5-6 mm. long, filaments glabrous, anthers about 0.5 mm. long; style including branches about

6 mm. long, the branches nearly 5 mm. long, the undivided part with hirsute and glandular hairs; ovary 1 mm. long, strongly compressed, ovate, hirsute and glandular, ovules 4; capsule 3 mm. long, elliptical, shortly hirsute and a little glandular, breaking free from the calyx readily; seeds 2, nearly 2 mm. long, ovate-lanceolate, plano-convex, sharply acute, light tan, rather coarsely pitted.

Phacelia marcescens is a very distinct entity which is restricted to a narrow transverse belt on the western slope of the Sierra Nevada from 4000 to 7000 ft. in the drainages of the Yuba and American rivers. It occurs to the north of *P. Quickii* and to the west and south of *P. humilis*. As indicated by descriptions and cited specimens, both *P. marcescens* and *P. Quickii* formed a large part of Brand's *P. humilis* (Das Pflanzenr. IV. 251: 102), but these species may be readily distinguished from *P. humilis* by their markedly glandular foliage, marcescent or tardily deciduous corollas, and glabrous filaments.

Representative specimens: all from CALIFORNIA: Bear Valley, Nevada Co., *Bolander in 1872* (G, type), *Jump in 1939* (CAS, DS, F, FP, G, NY, P, UC, US); Bowman Dam Road, Nevada Co., *MacFadden No. 12571* (CAS); Yuba River below Cisco, Placer Co., *Heller No. 12709* (CAS, DS, F, G, M, NY, US); Emigrant Gap, Placer Co., *M. E. Jones No. 3294* (CAS, DS, IU, M, NY, P, UC, US); American River, Placer Co., *von Geldern in 1912* (CAS).

7. PHACELIA QUICKII J. T. Howell, Leafl. West. Bot. 3:140. 1942.

P. Dociana Jepson & Hoover, Fl. Calif. 3:254 (1943).

Root annual; stems strictly erect and few-branched above or fastigiately branched from the base, 0.5-3.5 dm. tall, glandular and hirsutulous; leaves sometimes rosulate, generally mostly cauline, the lowest opposite, the upper alternate, lanceolate to oblong-linear, 0.6-4 cm. long, 0.2-1 cm. wide, glandular and hirsute above and below, the veins generally impressed above, margin more or less revolute, entire or very rarely dentate-lobed, acute, gradually narrowed at base into bordered petiole, petiole to 1.5 cm. long; racemes densely flowered, becoming elongate to about 1 dm. long, pedicels 1 mm. long; sepals unequal, in flower 2-4 mm. long, 0.3-0.8 mm. wide, in fruit generally strongly unequal, 3.5-7 mm. long, 0.3-1 mm. wide, narrowly linear to oblanceolate-spatulate, glandular and hirsute; corolla blue or lavender, tardily deciduous, at first campanulate but becoming tubular-contracted after anthesis, 3-5 mm. long, tube about 2 mm. long; corolla-scales 1 mm. long, narrowly oblong, the free edges of adjacent pairs connate; stamens 3-6 mm. long, generally a little exserted, filaments glabrous, anthers about 0.5 mm. long; style and branches 3.5-6 mm. long, branches 2.5-4.5 mm. long, style hirsutulous and glandular, the branches glandular at the base; ovary about 1 mm. long, glandular-hirsutulous, ovules 4; capsule globose-ovate, only a little longer than wide, 2-2.5 mm. long, hirsute and hirtellous, scarcely glandular, beak very short or almost none; seeds 2 or 3, turgidly and broadly ovate, obtuse or subacute, 1.3 mm. long, brown, coarsely pitted.

Open sandy flats and slopes of the Sierra Nevada, 4000 to 7200 feet from Eldorado County south to Fresno County, California.

Phacelia Quickii is the common representative of the *P. humilis* group on the middle western slope of the Sierra Nevada in the main forest belt. It is closely related to *P. marcescens,* but in *P. Quickii* the leaves are narrower and usually entire, the corolla is paler and less marcescent, the capsule is thicker and subglobose, and the seeds are more plumply ovate.

Representative specimens: all from CALIFORNIA: Emerald Bay, Lake Tahoe, Eldorado Co., *J. T. Howell No. 1166* (CAS); Ham's, Amador Co., *Hanson No. 1131* (DS, M); Douglas Station, Alpine Co., *Hoover No. 3642* (CAS, UC); Strawberry, Tuolumne Co., *Quick in 1931* (CAS, type, G, US); Mather, Tuolumne Co., *Keck No. 1107* (CAS, DS, G, M, P, RSA); Yosemite Valley, Mariposa Co., *J. T. Howell No. 16243* (CAS); Wawona, Mariposa Co., *J. T. Howell No. 60* (CAS); Ellis Meadow, Madera Co., *Quick in 1931* (CAS, G); Pine Ridge, Fresno Co., *Hall & Chandler* (DS, M, NY, UC, US); Florence Lake, Fresno Co., *Russell No. 63* (DS).

8. PHACELIA RACEMOSA (Kell.) T. S. Brandg., Zoë **2**:252. 1891.

Nama racemosum Kell., Proc. Calif. Acad. Sci. **5**: 51 (1873).
Phacelia namatoides Gray, Proc. Amer. Acad. **10**:317 (1875).

Root annual; stem erect, 0.3-1.5 dm. tall, the hypocotyle and first internode usually much longer than the upper part of the plant, the hypocotyle up to 4 cm. long and the first internode up to 5.5 cm. long, the stems glabrous and glaucous below, becoming finely glandular-pilose above, branching at the cotyledons or the first foliage leaves, sometimes several branches from the axil of a single leaf; cotyledons prominent, 0.5-1 cm. long, oblong or oblanceolate, connate-perfoliate at base; the lower foliage leaves opposite, the upper alternate, linear to lanceolate, oblanceolate or oblong, 1-3.5 cm. long, 0.1-0.6 cm. wide, scattered-hairy below, subappressed-hirsutulous above, hairs glandular and non-glandular, the margin broadly undulate or entire, apex subacute or obtuse, narrowed below to bordered petiole-like base; racemes to 4.5 cm. long, the lowest flowers distant, the uppermost approximate, the rachis more or less glandular-pilose, the pedicels 1-1.5 mm. long below, almost none above; calyx-segments in flower very unequal in length and width, 1.75-2.5 mm. long and 0.5-0.75 mm. wide in one flower, the two smallest segments linear, the two widest oblanceolate, in fruit somewhat accrescent, becoming 3-4 mm. long, hirsutulous and a little glandular; corolla very pale lavender, tubular-campanulate, 2.5-3 mm. long, the tube 1.5 mm. long; corolla-scales free, unequal in single corolla, the longest pair semi-elliptical below and extending above into a caudate free tip, the whole 0.5 mm. long; stamens 1-2 mm. long, the filaments with a few minute retrorse processes, anthers tiny, about 0.2-0.25 mm. long; style and branches 1-1.5 mm. long, the branches 0.66-1 mm. long, the style sparsely hairy; ovary 0.66 mm. long, hirsutulous, ovules 4; capsules subglobose, a little compressed, broader than long, 2.25-3 mm. long, hirsutulous and with a few glands, the undivided part of style persistent as a beak; seeds 4, 1.5-2 mm. long, rather finely pitted, dark brown, rounded on back, the faces flat, one narrow and one broad.

On the western slope of the northern and middle Sierra Nevada in California in the main forest belt from 5000 to 7600 ft.

The remarkable character of *P. racemosa* is the extreme development of the lower part of the stem in which the hypocotyl and first internode are markedly elongate. Not only are the cotyledons opposite but the first two foliage leaves are also opposite, and since branches generally arise from the axils of those leaves and the cotyledons, a very distinctive habit is produced. Heretofore the opposite leaves and branching have been used as distinguishing characters for the species, but the characters are not entirely diagnostic since the first two or four leaves above the cotyledons are opposite in all of the species of the *P. humilis* group. In certain plants of *P. humilis* itself, for example, this habit of growth is notably developed. In habit *P. racemosa* simulates *P. Pringlei,* but the two species may not be very closely related since the flowers are quite unlike in the two and *P. Pringlei* generally has more than four ovules in each ovary.

Representative specimens: all from CALIFORNIA: Eagle Lake, Lassen Co., *Austin in 1879* (UC); near Lassen Peak, Tehama Co., *Hermann No. 2541* (CAS, US); Jonesville, Butte Co., *E. B. Copeland in 1931* (CAS, DS, F, G, M, NY, P, RSA, UC, US); Long Lake Trail, 6600 ft., Plumas Co., *Head in 1920* (CAS); Summit Station, Nevada Co., *Heller No. 6981* (CAS, DS, G, M, NY, P, UC); Squaw Creek, Placer Co., *Eastwood No. 229* (CAS); Cisco, Placer Co., *Hall No. 8701* (CAS, DS, F, G, M, NY, P, UC, US); Fallen Leaf Lake, *Peirson No. 6294* (CAS, FP, UC); Bear River, Amador Co., *Hansen No. 1943* (DS, M, US); North Fork Stanislaus River, 7000 ft., Calaveras (?) Co., *Jussel in 1930* (CAS); Cow Creek, Tuolumne Co., *Quick No. 1852* (CAS); Glacier Point, Mariposa Co., *Hall No. 9146* (UC); Huntington Lake, Fresno Co., *A. L. Grant No. 1508* (P).

9. **Phacelia Greenei** J. T. Howell, spec. nov.

Annua; caulibus substricte erectis, 8-12 cm. altis, foliosis, plerumque supra pauci-ramosis, ramis valde adscendentibus, hirsutulis glandulosisque; foliis infimis proximis haud rosulatis, caulinis anguste oblongis ad oblanceolatis, 1.5-2.5 cm. longis, 3-5 mm. latis, integerrimis, supra strigulosis, infra hirsutulis et capitato-glandulosis, apice subobtusis, basi in petiolum brevem marginatum gradatim attenuatis, petiolis 0.5-1 cm. longis vel supra nullis; racemis foliis longioribus, nonnihil densifloris, usque ad 4.5 cm. longis, glanduloso-hirsutulis vel glanduloso-pilosis, pedicellis 1-3 mm. longis, valde adscendentibus; lobis calycis ad anthesin 2-3 mm. longis et 0.5-0.75 mm. latis, in fructu 3.5-5 mm. longis et 0.5-1 mm. latis, anguste oblongis ad oblanceolatis, subaequilongis, in latitudine paulo inaequalibus; corolla mature decidua, violacea, late rotata, 5-6 mm. longa, 7-9 mm. lata, lobis 2.5 mm. longis, rotundatis, integris; squamis 0.75-1 mm. longis, anguste oblongis, squamis jugorum vincinorum marginibus liberis connatis; staminibus exsertis, circa 5 mm. longis, filamentis sine pilis multas papillas retrorsas compressas ferentibus, antheris 0.75 mm. longis; stylo et ramis 6-6.5 mm. longis, ramis circa 4 mm. longis, stylo et basibus ramorum hirsutulis; ovario 1 mm. longo, praelonge pilosis, ovulis 4; capsula 3 mm. longa, 2 mm. lata, turgide ovata, infra rostrum prominens 1 mm. longum subacuta, pilis longis brevibusque et paucis glandibus capitatis tenuiter hirsuta, valvis in longitudinem sulcatis; seminibus 3 vel 4, oblongis, 1.75-2 mm. longis, 0.75-1 mm. latis, obtusis, fuscis, paulo tenuiter foveolatis.

Apparently known only from a single collection, *Greene No. 816,* collected

on June 5, 1876, near Yreka, Siskiyou Co., California (G, type; M, ND). The label of the specimen in Herb. Greene. gives the locality as Scott Valley but the label of the type bears Greene's comment, "on dry hillsides but scarce."

The affinities of this species are not readily apparent. Whereas it is properly included in the present treatment of the *Phacelia humilis* group because of the 4-ovulate capsule, it differs from all other members of the group in the broadly rotate corolla and it may not be as closely allied to the present group as to some species of the subgenus *Eutoca*. In fact the nearest relative of *P. Greenei* may be that form of *P. Pringlei* which is known chiefly if not exclusively from the mountains of Jackson Co., Oregon. There are several technical differences between them besides the number of ovules but the habital resemblance between the two is very suggestive and the character of the flowers is remarkably similar.

EXCLUDED VARIETIES

PHACELIA HUMILIS var. CALYCOSA Gray, Proc. Amer. Acad. 10:318 (1875); Bot. Calif. 1:507 (1876). This is *P. Purpusii* T. S. Brandg., to which should also be referred the manuscript name *P. trichostemoides* Greene which was published by Brand (Das Pflanzenr. IV. 251: 103) as a synonym of Gray's variety. Specimens bearing Greene's name have been examined in Herb. Greene. and Herb. Univ. Calif. The identity of Gray's variety has been discussed in Leafl. West. Bot. 3:162 (1942).

PHACELIA HUMILIS var. CONGDONII (Greene) Macbr., Contrib. Gray Herb. n. ser. 49:38 (1917). *P. Congdonii* Greene, Pittonia 5:22 (1902). The affinity of *P. Congdonii* is not with *P. curvipes* Torr. where Brand (op. cit., p. 115) referred it as a *"forma hispida,"* nor with the even more remotely related *P. humilis* where Macbride inadvisedly placed it as a variety. The plant seems to be a specifically distinct Sierran ally of the Coast Range *P. divaricata* (Benth.) Gray, from which it may be distinguished by the shorter stamens with non-glandular filaments, smaller corolla-scales, shorter styles, and long-pilose capsule. Specimens of *P. Congdonii* have been examined from Mariposa, Fresno, Tulare, and Kern counties, California.

II. Types of Phacelia in the Greene Herbarium

Greene named thirty-six new species and varieties of *Phacelia*, a greater number than any other botanist except Asa Gray, although a hasty census of Gray's work would seem to indicate that both named the same number of kinds. Because of the critical character of many of Greene's entities, it is generally necessary to examine authentic material in order to evaluate them properly. Since one cannot always be certain where the types of Greene's plants are to be found, I have prepared a list of *Phacelia* types in his herbarium where the types for all except five are to be found. In the following list, besides giving the collection data on the labels, I give under Greene's name all nomenclatural combinations in which his epithet may have appeared, and I have added personal comments or additional data which I regard pertinent.

Except in one or two instances, I do not express an opinion as to the taxonomic status of Greene's entities—that is a matter to be treated in systematic revisions and monographs. Since I have grouped the phacelias by relationship, I have prepared an index to Greene's names in order to facilitate the use of the list.

A. Greene's Species Related to Phacelia magellanica

1. PHACELIA BIOLETTII Greene, Pittonia 5:23. 1902.

Type. Sequoia Canyon, *F. T. Bioletti,* July, 1891.

Bioletti undoubtedly collected the type in the redwood region of the Oakland Hills in western Contra Costa County, California. Two specimens of *P. Biolettii* in Herb. Calif. Acad. Sci. are: Oakland redwoods, *Bolander;* near Redwood Peak, *J. T. Howell No. 17005.*

As Greene remarks in the original description, *P. Biolettii* is related to *P. nemoralis* Greene, from which it differs most obviously in the violet-lavender corolla. Although Brand recognizes *P. nemoralis* as a species, he does not give an adequate estimate of *P. Biolettii* when he gives it as a synonym of *P. magellanica* (Lam.) Cov. (1913, p. 95).

2. PHACELIA COMPACTA Greene ex Brand, Univ. Calif. Publ. Bot. 4:217. 1912.

P. compacta Greene ex Baker, West Amer. Plants 18 (1902), nomen nudum. *P. magellanica* (Lam.) Cov. subsp. *barbata* Brand f. *compacta* (Greene) Brand, l.c. *P. leucophylla* Torr. var. *compacta* (Greene) Macbr., Contrib. Gray Herb., n. ser., 49: 34 (1917). *P. heterophylla* Pursh var. *compacta* (Greene) Jeps., Man. Fl. Pl. Calif. 819 (1925).

Type. Spooner, Douglas County, Nevada, *C. F. Baker No. 1142,* June 23, 1902.

In Dundas' recent revision of the *P. californica* group, the "key-character" for recognizing *P. leucophylla* var. *compacta* is "basal leaves pinnatifid" (1935, p. 162). In the type all of the leaves are entire. The corollas of plants in this relationship are usually lavender-violet but it was not possible to tell what might have been the color of the corollas in the type.

3. PHACELIA DASYPHYLLA Greene ex Macbride, Contrib. Gray Herb., n. ser., 49:35. 1917.

P. dasyphylla Greene ex Brand, Das Pfanzenr. IV. 251: 97 (1913), in syn. *P. heterophylla* Pursh var. *dasyphylla* (Greene) Jepson, Man. Fl. Pl. Calif. 819 (1925).

Type. Mt. Whitney, 13,000 ft., *Culbertson in C. F. Baker distribution No. 4355,* Aug. 15, 1904.

In specimens of the type collection the corollas are deep lavender.

4. PHACELIA EGENA Greene ex Brand, Univ. Calif. Publ. Bot. 4:218. 1912.

P. magellanica (Lam.) Cov. subsp. *barbata* Brand f. *egena* (Greene) Brand, l.c.

P. californica Cham. f. *egena* (Greene) Macbr., Contrib. Gray Herb., n. ser., **49**: 37 (1917). *P. californica* Cham. var. *egena* (Greene) Dundas, Bull. S. Calif. Acad. Sci. **33**: 161 (1935).

Type. South Fork of Kaweah River at 7000 ft., *Culbertson in C. F. Baker distribution No. 4415*, July 21, 1904.

Leaves entire or with pair of tiny leaflets below the larger terminal segment; corolla whitish.

5. PHACELIA IMBRICATA Greene, Erythea **1**:127. 1893.

P. californica Cham. var. *imbricata* (Greene) Jepson, Fl. W. Mid. Calif. 439 (1901).

Type. Near St. Helena, Napa County, California, *Greene*, July, 1891.

The type represents the plant that is so common in the mountains immediately north of San Francisco Bay with large ovate fruiting sepals and with whitish flowers. The corolla is tubular-campanulate with the lobes erect in flower and somewhat incurved in age. The pubescence of the plant is hirsute and hirsutulous, not at all glandular. In the original description, Greene described the corolla as "bluish" but this is undoubtedly a mistake since the plant obviously has the characteristic whitish corollas which become sordid in age. A form of *P. californica* Cham. with pale "bluish" corollas occurs in the same region but in that plant the fruiting calyx is quite different.

6. PHACELIA MUTABILIS Greene, Erythea **4**:55. 1896.

P. nemoralis Greene var. *mutabilis* (Greene) Macbr., Contrib. Gray Herb., n. ser., **49**: 37 (1917).

One of the things which I especially hoped to see at the Greene Herbarium was the type of this phacelia. From Greene's description it had been evident to me for a number of years that the name was to be applied to a widespread phacelia of the middle and upper forests of the Sierra Nevada in California where it was rather common and quite variable. Several variants within the broader limits of the entity had received nomenclatural recognition and the extremes of variation closely approached, or were perhaps confluent with, yet other entities which had been regarded as more or less distinct. Hence, it was a real disappointment to find that Greene had not indicated a type in the rather considerable suite of specimens he had determined as *P. mutabilis*.

In his characteristic way, Greene gave a broad distributional account of his species in the original description: "common towards Castle Peak, and southward to at least Alpine Co., also northward to the borders of Oregon; seldom or never passing to the westward slope of the Sierra." This statement is not very helpful when one compares with it critically the specimens that might have been available to Greene when he described the plant. There is no specimen nearer Castle Peak than "near Summit Station" and all the Sierran specimens are apparently from the western slope. From the diagnosis one does not find a clue to a type either, since here, too, Greene undoubtedly had

several specimens in mind. Although he describes the species as "biennial," several of the plants labelled *P. mutabilis* are short-lived perennials.

The following ten collections, all from California, were determined by Greene as *P. mutabilis* and were collected before March, 1896, the date of publication: Big Meadows, Plumas County, *Mrs. R. M. Austin*, June, 1880 (perennial, corolla bluish); Calaveras County, *Greene*, July, 1889 (biennial, corolla ochroleucous); Mammoth, Mono County, *Coville & Funston No. 1824*, July 22, 1891 (corolla lavender); Forestdale, Big Valley Mts., *M. S. Baker*, June 20, 1893 (biennial, corolla lavender); Nevada County, *Carpenter in 1893* (perennial, corolla whitish); Summit Station, *Greene*, July, 1893 (perennial); Big Valley Mts., Modoc County, *Baker & Nutting in 1894* (biennial, corolla lavender); Warner Range, Modoc County, *Mrs. R. M. Austin*, July, 1895 (biennial, corolla bluish); Blue Canyon, Placer County, *Greene*, July 21, 1895 (biennial, corolla whitish); near Summit Station, *Greene*, July 23, 1895 (biennial, corolla pale lavender).

There is no way of telling when these specimens were labelled *P. mutabilis* by Greene, but from them it is obvious that earlier or later he intended the name to apply to the common phacelia of the Sierra Nevada which has been referred more recently to *P. heterophylla* Pursh, *P. nemoralis* Greene, or their varieties. Since several minor entities or strains are represented which have been variously interpreted, it seems desirable at this time to fix the application of Greene's name by designating a collection in his herbarium as the type. For this purpose, I choose the collection last-cited above, the one from near Summit Station, collected by Greene in 1895. This is the collection which came from as near Castle Peak as any (perhaps from the slope of the mountain itself), while it and the one from Blue Canyon were obtained by Greene in the summer immediately preceding the publication of the species. A collection made by Heller (*No. 12890*, Herb. Calif. Acad. Sci.) at Summit Station in open places in coarse granite sand at an elevation of 6960 ft. corresponds closely with the type.

At this time it seems appropriate to indicate that the type of *P. magellanica* f. *griseophylla* Brand (Univ. Calif. Publ. Bot. 4:218, 1912) represents a plant that is very closely related to *P. mutabilis*.[1] For the type of Brand's form, I have chosen the first-cited specimen, that of K. Brandegee collected at Sisson, Siskiyou County, in July, 1887 (Herb. Univ. Calif. No. 107348).

Brand cites two other specimens: the second, *Heller No. 8755* from Red Clover Valley, Plumas County, is not entirely typical according to Brand; while the third, a collection by K. Brandegee from Alta Meadows, Tulare County, consists of some plants with hairy filaments and some with glabrous filaments. Although this southern Sierran plant is closely related to *P. mutabilis*, it may be varietally distinct. Brand's f. *griseophylla* was treated as a variety

1 By this statement I mean that if the entity represented by the type of *P. mutabilis* is accepted as a taxonomic unit, I would regard *P. magellanica* f. *griseophylla* the same. I believe it is wrong, however, to give the impression that the two names are exactly synonymous when one is considering a group as polymorphic as this. Time and again field experience has shown that one cannot say that all plants growing even in a single restricted colony are exactly the same.

of *P. heterophylla* Pursh by Macbride (1917, p. 35) and as a synonym of *P. heterophylla* Pursh var. *typica* Dundas by Dundas (1935, p. 154).

It also seems proper to include here a brief consideration of *P. nemoralis* Greene var. *pseudohispida* Brand (1912, p. 219). The type, *M. S. Baker No. 344*, collected at Stalkers, Shasta County, California, July 10, 1898 (Herb. Univ. Calif. No. 73686), is a tall laxly branched plant with large thin leaf-blades and loosely flowered elongate flowering branches. As has been pointed out by Dundas (1935, p. 167) under the name *P. pinnata* (R. & P.) Macbr. var. *pseudohispida* (Brand) Dundas, the plant is the same as *P. mutabilis* Greene. The type was originally labelled *P. mutabilis* (undoubtedly after a determination by Greene), and the M. S. Baker collection of 1898 of *P. mutabilis* in Herb. Greene. is probably a duplicate, although the locality and collector's number are lacking from Greene's specimen. The type of var. *pseudohispida* with its unusually lax habit and inflorescence undoubtedly represents a robust shade-form of *P. mutabilis*. It corresponds closely to a specimen in Herb. Calif. Acad. Sci. which I collected in 1926 near Prattville, Plumas County, California, *J. T. Howell No. 2098*.

In concluding these remarks on *P. mutabilis*, I shall bring together under that name the several names which I have considered here and which I regard as synonyms. As I indicated in my introductory remarks, this does not mean that *P. mutabilis* is here accepted as a species, it is merely a convenient way in which to assemble a considerable amount of synonymy discussed at this time.

PHACELIA MUTABILIS Greene, Erythea **4**:55. 1896.

P. magellanica (Lam.) Cov. f. *griseophylla* Brand, Univ. Calif. Publ. Bot. **4**: 218 (1912). *P. nemoralis* Greene var. *pseudohispida* Brand, op. cit., 219. ? *P. nemoralis* x *hispida* Brand, Das Pflanzenr. IV. **251**: 101 (1913). *P. heterophylla* Pursh var. *griseophylla* (Brand) Macbr., Contrib. Gray Herb., n. ser., **49**:35 (1917). *P. nemoralis* Greene var. *mutabilis* (Greene) Macbr., op. cit., 37. *P. heterophylla* Pursh var. *typica* Dundas, Bull. S. Calif. Acad. Sci. **33**: 154 (1935) in part. *P. pinnata* (R. & P.) Macbr. var. *pseudohispida* (Brand) Dundas, op. cit., 167. *P. magellanica* (Lam.) Cov. var. *griseophylla* (Brand) Jepson, Fl. Calif. **3**:247 (1943).

7. PHACELIA NEMORALIS Greene, Pittonia **1**:141. 1887.

Type. Oakland Hills, California, *Greene*, July 21, 1887.

The only other specimens labelled *P. nemoralis* besides the type are several collections from the Sierra Nevada which should have been transferred to the *P. mutabilis* folder after the latter species was described. *Phacelia nemoralis* originally included the Sierran plant as well as the Coast Range plant, but from Greene's discussion of *P. mutabilis* (1896, p. 56), it is clear that the name *P. nemoralis* was later restricted to the coastal plant.

8. PHACELIA VIRGATA Greene, Erythea **4**:54. 1896.

P. magellanica (Lam.) Cov. f. *virgata* (Greene) Brand, Univ. Calif. Publ. Bot. **4**: 219 (1912). *P. californica* Cham. var. *virgata* (Greene) Jepson, Man. Fl. Pl. Calif. 820 (1925).

Type. Near Yreka, Siskiyou County, California, *Greene No. 832,* June 7, 1876.

PHACELIA VIRGATA Greene var. AMPLIATA Greene, Erythea 4:55. 1896.

Type. Washoe Mts. south of Truckee, California, *Greene,* July 25, 1895.

A specimen which I collected at Emerald Bay, Lake Tahoe, Eldorado County, California, was compared with Greene's type, and although it agreed in general, it was noted as being more robust in habit.

PHACELIA VIRGATA Greene var. BERNARDINA Greene, Erythea 4:55. 1896.

P. magellanica (Lam.) Cov. f. *bernardina* (Greene) Brand, Univ. Calif. Publ. Bot. 4: 218 (1912). *P. californica* Cham. f. *bernardina* (Greene) Macbr., Contrib. Gray Herb., n. ser., 49: 36 (1917). *P. californica* Cham. var. *bernardina* (Greene) Jepson, Man. Fl. Pl. Calif. 820 (1925).

Type. San Bernardino, San Bernardino County, California, *S. B. & W. F. Parish,* June 1, 1887.

The following specimen in Herb. Calif. Acad. Sci. was compared with the type: *S. B. Parish No. 7123,* collected on dry mesas in the San Bernardino Valley, May 30, 1909.

B. Allies of Phacelia distans Named by Greene

9. PHACELIA AMMOPHILA Greene ex Brand, Univ. Calif. Publ. Bot. 4:216. 1912.

P. ammophila Greene ex Baker, West Amer. Plants 2: 15 (1903), nomen nudum. *P. distans* Benth. var. *eu-distans* Brand subvar. *ammophila* (Greene) Brand, l.c.

Type. Sand hills, Antioch, Contra Costa County, California, *C. F. Baker No. 2806,* May 28, 1903.

10. PHACELIA ARTHURI Greene, Pittonia 1:224. 1888.

The only specimen of this plant in Herb. Greene. does not carry the data given for the type in the original description. Whereas the type was collected by Arthur B. Simonds in Oakland, California, in 1887, data on the specimen in Herb. Greene. give Greene as the collector in 1888. Nevertheless it seems likely that this specimen is the type since it agrees with the original description as to the sterility of the plant and its distinctive morphology. Brand (1913, p. 92) indicates that he examined a specimen of Simonds' collection in Herb. De Candolle.

11. PHACELIA COMMIXTA Greene, Pittonia 5:21. 1902.

Type. San Bernardino, San Bernardino County, California, *S. B. & W. F. Parish,* May 15, 1891.

Specimens of two related but unlike plants are on the type sheets: the one on the left being like the form of *P. distans* Benth. which is so common and

characteristic of the washes of southern California; the one on the right being the actual type as was clearly indicated by Greene. In the original description, Greene allies his plant with *P. tanacetifolia* Benth., but the relation is certainly with *P. distans*, since the fruiting sepals of the type are markedly unequal and the "stamens wholly included."

12. PHACELIA LEPTOSTACHYA Greene, Erythea 2:190. 1894.

P. distans Benth. var. *eu-distans* Brand subvar. *leptostachya* (Greene) Brand, Das Pflanzenr. IV. **251**: 89 (1913).

Type. Alameda, Alameda County, California, *Greene*, June 16, 1892.

A collection which I made in the Berkeley Hills, Alameda County, was noted as comparing favorably with the type.

13. PHACELIA SCABRELLA Greene, Pittonia 1:35. 1887.

P. distans Benth. var. *scabrella* (Greene) Brand, Das Pflanzenr. IV. **251**: 90 (1913).

Type. Island of San Miguel, California, *Greene*, Sept., 1886. Isotype in Herb. Calif. Acad. Sci.

Munz (1935, p. 410) gives *P. scabrella* as a synonym of *P. ramosissima* Dougl. var. *subsinuata* (Greene) Macbr. but this is surely a mistake.

C. Greene's Segregates in Phacelia ramosissima Dougl. sens. lat.

14. PHACELIA BIFURCA Greene, Pittonia 5:18. 1902.

Type. Tehachapi, Kern County, California, *Greene*, June 22, 1889.

15. PHACELIA DECUMBENS Greene, Pittonia 5:17. 1902.

P. ramosissima Dougl. f. *decumbens* (Greene) Brand, Univ. Calif. Publ. Bot. Bot. **4**: 215 (1912).

Type. Near Yreka, Siskiyou County, California, *Greene No. 896*, June 28, 1876; southern flanks of Uncle Sam Mt. (i.e., Mt. Konocti), Lake County, California, *Jepson*, July-Aug., 1892. On the latter Greene has written: "Description of capsule and seeds was from this."

16. PHACELIA EREMOPHILA Greene, Pittonia 5:20. 1902.

P. ramosissima Dougl. var. *eremophila* (Greene) Macbr., Contrib. Gray Herb., n. ser., **49**: 31 (1917).

Type. West Humboldt Mts., Pershing County, Nevada, *Greene*, July, 1894.

17. PHACELIA FASTIGIATA Greene, Pittonia 5:18. 1902.

Type. Kern County, California, *Palmer & Wright No. 205*, in 1888.

Brand (1913, p. 92) cites *Palmer 205* from Long Meadow, Tulare County,

as the type of *P. fastigiata*. Whereas the specimens in Greene's herbarium represents an inflorescence from a robust plant which I interpreted as being related to *P. ramosissima* var. *suffrutescens* (Parry) Parry, Brand (1913, p. 92) gives *P. fastigiata* as a synonym of *P. ramosissima* f. *decumbens* which is usually a more slender montane plant. Brand's interpretation is probably correct if the type actually came from the high southern Sierra Nevada in Tulare County. Following Greene's original description, Macbride (1917, p. 30) also regarded *P. fastigiata* a synonym of var. *suffrutescens*. The correct disposition of *P. fastigiata* must await further detailed study of Greene's type.

18. PHACELIA POLYSTACHYA Greene, Pittonia 5:19. 1902.

Type. Witch Creek, San Diego County, California, *R. D. Alderson in 1893*.

19. PHACELIA SUBSINUATA Greene, Pittonia 5:19. 1902.

P. ramossissima Dougl. var. *subsinuata* (Greene) Macbr., Contrib. Gray Herb., n. ser., **49**: 30 (1917).

Type. San Rafael Mts., Santa Barbara County, California, *John Spence in 1886*.

The type looks like a shade form with shallowly and subsinuately lobed leaves with the lobes rounded and obtuse. Since the type is merely a branchlet about 6 inches long, it seems probable that the lower leaves were pinnately divided as is usual in the *P. ramosissima* group.

Macbride (1917, p. 30) has already given a revisional estimate of Greene's segregates in *P. ramosissima* and undoubtedly his reliance on characters of vesture and fruiting sepals aligns the several entities in a natural taxonomic sequence. While studying in the Greene Herbarium, I prepared a synopsis of quantitative data obtained solely from the type specimens. This synopsis, which is in the form of an artificial key, I present here, not as an indication of real entities, but as a means of indicating quantitative data not obtainable from the original descriptions.

A. Corollas small, 4-5 mm. long; sepals in immature fruit 5 mm. long.
  B. Stem robust; leaves pinnately divided ..... *P. polystachya*
  B. Stem slender; leaves with ample broadly lobed blade, the lobes rounded and obtuse ..... *P. subsinuata*
A. Corollas larger, 5-10 mm. long; sepals in fruit 7-10 mm. long.
  C. Corollas 5-7 mm. long; sepals in fruit 7-8 mm. long; stems robust.
    D. Leaves finely and sharply cut; branches of inflorescence ascending to nearly horizontal ..... *P. bifurca*
    D. Leaves less finely cut; branches of inflorescence more strongly ascending ..... *P. fastigiata*
  C. Corollas 8-10 mm. long; sepals in fruit 7-10 mm. long; stems slender.
    E. Leaves less finely cut; sepals in fruit 10 mm. long ..... *P. eremophila*
    E. Leaves more finely cut; sepals in fruit 7-8 mm. long ..... *P. decumbens*

D. Miscellaneous Species by Greene in Phacelia § Euphacelia

20. PHACELIA CICUTARIA Greene, Pittonia 5:20. 1902.

P. hispida (Gray) Gray var. *genuina* Brand subvar. *cicutaria* (Greene) Brand, Univ. Calif. Publ. Bot. **4**: 215 (1912). *P. hispida* (Gray) Gray var. *cicutaria* (Greene) Macbr., Contrib. Gray Herb., n. ser., **49**: 28 (1917).

Type. Knights Ferry, Stanislaus County, California, *F. W. Bancroft*, Apr. 9, 1895.

As I have recently indicated (Leafl. West Bot. 3:119), Greene's name must replace *P. hispida* Gray (1878), not Buckley (1862), if one follows the presently accepted broad interpretation of Gray's species.

21. PHACELIA COERULEA Greene, Bull. Torr. Bot. Club 8:122. 1881.

Type. Near Silver City, Grant County, New Mexico, *Greene*, May, 1880.

Although Greene gives no indication of a type collection in the original description, the specimen in Herb. Greene. should undoubtedly be regarded the type in spite of the fact that Voss has recently "designated" a type for the species in Herb. Gray. (1937, p. 85).

22. PHACELIA HETEROSEPALA Greene, Pittonia 5:21. 1902.

P. hispida (Gray) Gray var. *genuina* Brand subvar. *heterosepala* (Greene) Brand, Univ. Calif. Publ. Bot. **4**:215 (1912). *P. hispida* (Gray) Gray var. *heterosepala* (Greene) Voss, Bull. S. Calif. Acad. Sci. **33**: 173 (1935). *P. cicutaria* Greene var. *heterosepala* (Greene) J. T. Howell, Leafl. West. Bot. **3**: 120 (1942).

Type. Iron Canyon, Butte County, California, *Mrs. R. M. Austin*, May, 1896. Isotype in Herb. Univ. Calif.

Greene has labelled Mrs. Austin's collection "the actual type," while a second specimen collected by Hansen in 1894 he has labelled "Part of the 'type,' but not typical." Hansen's collection is without locality data.

23. PHACELIA INCONSPICUA Greene, Erythea 3:24. 1895.

Type. West Humboldt Mts., Pershing County, Nevada, *Greene*, July 18, 1894.

This species is apparently known only from Greene's collection which is represented in Herb. Greene. by eight plants mounted on three sheets.

24. PHACELIA THERMALIS Greene, Erythea 3:66. 1895.

P. ciliata Benth. var. *thermalis* (Greene) Jepson, Man. Fl. Pl. Calif. 824 (1925).

Type. Little Hot Springs Valley, Modoc County, California, *Baker & Nutting*, June 4, 1894. Isotype in Herb. Calif. Acad. Sci.

E. Greene's Species in Phacelia § Eutoca

25. PHACELIA ALDERSONII Greene, Pittonia 5:22. 1902.

Type. Witch Creek, San Diego County, California, *R. D. Alderson No. 21*, in 1883. Isotype in U.S. Nat. Herb.

This plant seems definitely referable to *P. Davidsonii* Gray, differing from the type of Gray's species in its entire leaves and somewhat larger corollas. From Greene's description of the "fine pubescence" of *P. Aldersonii*, one might think that its vesture is markedly different from that of *P. Davidsonii*, but an examination of the type disclosed the presence of some of the hirsute hairs usual in *P. Davidsonii*. The corolla of *P. Aldersonii* is 8 mm. long.

26. PHACELIA CONGDONII Greene, Pittonia 5:22. 1902.

P. humilis T. & G. var. *Congdonii* (Greene) Macbr., Contrib. Gray Herb., n. ser., **49**: 38 (1917).

Type. Buckeye, Mariposa County, California, *J. W. Congdon*, Apr. 25, 1895. Isotype in Herb. Dudley., Stanford University.

The stems of the type specimen are up to 2 dm. long. In this more robust habit, the type is more like the plants from Kern County than the smaller slenderer plants that are more common farther north in Fresno and Mariposa counties.

27. PHACELIA NEMOPHILOIDES Greene, Pittonia 5:23. 1902.

Type. Southern slope of the San Bernardino Mts., San Bernardino County, California, 4000-6000 ft., *Parish No. 3771*, June 29-30, 1895. Isotypes in U. S. Nat. Herb. and Herb. Univ. Calif.

This is the large-flowered form of *P. Davidsonii* Gray which was described by Parish as *P. Davidsonii* var. *macrantha* (Erythea 6:90).

28. PHACELIA SUAVEOLENS Greene, Pittonia 1:223. 1888.

Type. Petrified Forest, Sonoma County, California, *Greene*, Aug. 31, 1888.

The type specimen is without the lower leaves which in the original description are described as having "some lyrate lobes at or below the base of the main blade." I have seen no specimens with leaves so deeply lobed (cf. Howell, 1943, p. 5).

29. PHACELIA TRICHOSTEMOIDES Greene ex Brand, Das Pflanzenr. IV. 251: 103 (1913), in synonymy.

Type. *M. S. Baker in 1893*. Undoubtedly this is Baker's collection from Stalkers, Shasta County, California, of which there is a specimen so-labelled in Herb. Univ. Calif. Brand (l.c.) published Greene's name as a synonym of *P. humilis* T. & G. var. *calycosa* Gray. Both Gray's and Greene's types are referable to *P. Purpusii* T. S. Brandg. (cf. Howell, 1942, p. 162).

F. Phacelia Types not Found in the Greene Herbarium

30. PHACELIA FLORIBUNDA Greene, Bull. Calif. Acad. Sci. 1:200. 1885.

Greene's collection from "lower parts of Guadalupe Island," Lower Cali-

fornia, was probably lost in the California Academy of Sciences in the San Francisco earthquake and fire in 1906.

31. PHACELIA FRIGIDA Greene, Pittonia **4**:39. 1899.

P. magellanica (Lam.) Cov. subsp. *barbata* Brand f. *frigida* (Greene) Brand, Univ. Calif. Publ. Bot. **4**:218 (1912). *P. heterophylla* Pursh f. *frigida* (Greene) Macbr., Contrib. Gray Herb., n. ser., **49**: 35 (1917). *P. heterophylla* Pursh var. *frigida* (Greene) Jepson, Man. Fl. Pl. Calif. 819 (1925). *P. magellanica* (Lam.) Cov. var. *frigida* (Greene) Jepson, Fl. Calif. **3**:248 (1943).

The type, collected by C. H. Merriam on Mt. Shasta, Siskiyou County, California, Aug. 3, 1898, is probably in the U. S. National Herbarium. Greene determined as *P. frigida* a specimen collected by Jepson "near the snow line, Mt. Shasta," Aug. 4, 1894. This specimen is probably part of the type collection of *P. heterophylla* Pursh var. *pygmaea* Jepson (Man. Fl. Pl. Calif. 819, —1925).

32. PHACELIA RUPESTRIS Greene, Leafl. Bot. Obs. **1**:152. 1905.

P. congesta Hook. var. *rupestris* (Greene) Macbr., Contrib. Gray Herb., n. ser., **49**: 25 (1917).

The type is *Metcalfe No. 1012*, collected 1 mile west of Hillsboro, in the "foothills of the Black Range," Sierra County, New Mexico. The type is perhaps in the U. S. National Herbarium. There is an isotype in Herb. Calif. Acad. Sci.

33. PHACELIA UMBROSA Greene, Erythea **2**:191. 1894.

P. hispida (Gray) Gray var. *umbrosa* (Greene) Brand, Das Pflanzenr. IV. **251**: 88 (1913).

According to Brand (l.c.), the type is in Herb. Univ. Calif. It was collected by C. R. Orcutt in the northern part of Lower California in 1885.

34. PHACELIA URTICACEA Greene ex Brand, Das Pflanzenr. IV. 251: 99 (1913), as synonym of *P. magellanica* (Lam.) Cov. f. *heterophylla* (Pursh) Brand.

No specimen has been seen which Greene called *P. urticacea*.

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III. Studies in Cirsium

Several of the most perplexing problems connected with Californian thistles have centered in the group of plants originally referred by Asa Gray to his *Cnicus Breweri* var. *Vaseyi* (1884, p. 404). Greene in 1893 and again in 1897 began the elucidation of the *Vaseyi* complex but the situation was later complicated by diverse and sometimes mistaken opinions on the typification of the several entities involved. For a number of years I have known of the difficulties and ambiguities, since scarcely a season passed but that collections from some part of middle or northern California raised the question of names. Hence, it was with real satisfaction that I was able to examine in the Greene Herbarium specimens which have made possible a systematic review of these vexatious problems. And, incidentally, in examining Greene's entire collection of *Cirsium*, it was gratifying to find in his *Carduus Macounii* the answer to yet another of my thistle problems.

A. The Macoun Thistle

In 1931, along the road between Mt. Baker and Bellingham, Washington, I collected two thistles. The first I recognized as *Cirsium edule* Nutt.; the second, amply distinct in habit, vesture, inflorescence, and flowers, was new to me. Later in Mt. Rainier National Park and again on Mt. Angeles, I collected the same thistle, always readily separable from *Cirsium edule* by its much more attractive and brightly colored heads. On my return to San Francisco,

I found that the thistle had been confused with *Cirsium edule* by Piper and by Petrak (Piper, 1906, p. 610, and Petrak, 1917, p. 318, at least as to *Sandberg & Leiberg No. 626*), and apparently it has not been distinguished from Nuttall's plant by any of the workers on the flora of southern British Columbia or western Washington (cf. Howell, 1903, p. 383; Piper and Beattie, 1915, p. 395; Henry, 1915, p. 323; St. John and Hardin, 1929, p. 94; St. John and Warren, 1937, p. 984; G. N. Jones, 1936, p. 258, and 1938, p. 168; Muenscher, 1941, p. 129). Thinking that the thistle might be *Cirsium Hallii* (Gray) Petrak, I had the privilege of borrowing the type of that Oregonian species from the Gray Herbarium but it was found to represent a different plant. More recently while examining types of thistles in the Greene Herbarium, I found the plant which I had collected more than eleven years before under the name *Carduus Macounii* Greene (1902, p. 38).

Petrak treats this species in that part of his revision entitled "Zweifelhafte oder mir unbekannte Arten und Hybriden" (1917, pp. 538-567). There he gives a brief diagnosis of the plant that is adapted from the original description, and, after remarking that Greene in his original description does not indicate the relationship of the plant, he states that he thinks it may be a member of the "*Undulata*-Gruppe." It was Petrak's general practice to transfer to *Cirsium* the names of plants described in *Carduus* or *Cnicus* even if the identity of a particular plant was unknown or its status doubtful, but in the case of *Carduus Macounii* the transfer is not made, probably due to an oversight in proofreading.

In the year of Petrak's revision, however, Rydberg (1917, p. 1007) transferred the name to *Cirsium*, although from his key and description it would seem that he, too, had a very inadequate idea of Greene's entity. It may be that what Rydberg describes is a plant from the Rocky Mountains and one quite different from the plant named by Greene; or it would seem even more likely from his descriptions of *Cirsium edule* and *Cirsium Macounii*, as well as from his key to the species, that he interchanged the characters of the two species in several important details.

From *Cirsium edule*, with which Greene's species has been so generally confused, *Cirsium Macounii* may be separated by a number of excellent characters. These are outlined in the following synopses:

Cirsium edule.—Leaves generally arachnoid-tomentose below; heads 2.5-3 cm. high; the inner phyllaries not very rigid and rather broadish up to the merely acerose tip; corolla dull rosy-purple, straight, only slightly exserted from the involucre, the linear-filiform lobes capitellate-enlarged at apex, 2-3.5 mm. long, the throat 3-5 mm. long and the tube 12-16 mm. long; anther-appendage narrow, about 0.5 mm. long, the filaments minutely if at all papillate; style only slightly exserted (to about 1.5 mm.); achene 3.5-4 mm. long, the pericarp finely undulate-marked and somewhat shiny, top of achene yellowish and bony-rimmed.

Cirsium Macounii.—Leaves glabrate or glabrous below except on midrib;

heads 3-4 cm. high; the inner phyllaries slender, rigid, long-spinose-pointed; corolla bright purplish-rose, outwardly curving and long-exserted from the involucre, the lobes broader and not capitellate, 4-5 mm. long, the throat 5-6 mm. long, and the tube 7-8 mm. long; anther-appendages wide and 2 mm. long, the filaments conspicuously and abundantly papillate; style becoming conspicuously exserted (up to 5 mm.); achene 5-6 mm. long, the pericarp dull, finely striate but not undulate-marked, top of the achene only little lighter than the body.

Where the two species grew together below Mt. Baker where I first distinguished them, I noted that they were very distinct in habit: whereas the plants of *Cirsium Macounii* were only 4 to 6 feet tall and were widely and loosely branched with heads solitary or congested, the plants of *Cirsium edule* were 6 to 8 feet tall and were mostly unbranched, or if branched above, the branches were short and erect-fastigiate, and the heads were capitate-congested. Greene described his species as perennial. I believe the plant is only biennial; certainly it is monocarpous.

The following collections of *Cirsium Macounii* have been studied in Herb. Greene. (ND) and Herb. Calif. Acad. Sci. (CAS). BRITISH COLUMBIA: Chilliwack Valley between lat. 49° and 49°10′ and long. 121°25′ and 122°, *Macoun No. 26451*, collected Aug. 2, 1901, alt. 1800 ft., and *Macoun No. 26452*, collected June 13, 1901, alt. 500 ft. (ND); Lake House, Skagit River, *Macoun No. 76943* (ND). WASHINGTON: Nooksack River Valley, 10 miles east of Glacier, Whatcom County, *J. T. Howell No. 7383* (CAS, ND); Cascade Tunnel, Chelan County, *M. E. Jones in 1911* (CAS); Nason Creek, Chelan County, *Sandberg & Leiberg No. 626* (CAS); Embro, King County, *Otis No. 743* (CAS); Inter Fork White River, Mt. Rainier, Pierce County, *J. M. Grant in 1925* (CAS); Reflection Lake, Mt. Rainier National Park, Lewis County, *J. T. Howell No. 7407* (CAS), *L. S. Rose No. 40772* (CAS); American River Canyon above Union Creek, Yakima County, *Eastwood & Howell No. 2990* (CAS); Mt. Angeles, 4500 ft., Clallam County, *J. T. Howell No. 7467* (CAS). Rydberg (1917, p. 1007) in his distribution of *Cirsium Macounii* gives Alberta and Montana as well as British Columbia and Washington, but I have seen no specimens from the Rocky Mts. which I would refer to *Cirsium Macounii*.

B. Greene's Truckee Thistle

In August, 1883, Greene collected a small-headed thistle near Truckee, Nevada County, California, which he named a decade later *Carduus undulatus* var. *nevadensis* (1893, p. 361) and still later *Carduus inamoenus* (1897, p. 479). The identity of this plant has puzzled me for a number of years since no specimens which I had from the east slope of the northern Sierra Nevada seemed to agree with Greene's descriptions, and it was only after examining Greene's type at Notre Dame that I fully appreciated his plant. Although the type for the variety is definitely the plant from Truckee, a few words should be added concerning the typification of *Carduus inamoenus*. In the original description of the latter, Greene gives the distribution of his new species as "common on the eastern foothills of the Sierra Nevada, from Plumas Co. southward to the Truckee Valley. It forms a part of the *Cnicus Breweri Vaseyi* of Gray, but is not the plant of Vasey's collecting. It is also my *C. undulatus Nevadensis*."

Gray's *Cnicus Breweri* var. *Vaseyi* (1884, p. 404) consisted of three

different entities which were denoted in the following sequence: plants of Plumas and Sierra counties collected by Mrs. Ames and by Lemmon; "a remarkably glabrate form" from Mt. Tamalpais, Marin County, by Vasey; and "a robust form" from the Suisun Marshes by Greene. Each of these "forms" was destined to be recognized as a distinct species and the matter has been further complicated because authors have not agreed on the typification. Greene was the first to segregate a species from this *Vaseyi* complex, the Suisun "form" which he called *Carduus hydrophilus* (1893, p. 358). It is obvious from Greene's distributional note, then, that, when he named *Carduus inamoenus* five years later, it was his intention that his entity should include the first-described element in Gray's variety. Greene, however, was mistaken in regarding the thistle collected by Ames and by Lemmon the same as his *Carduus undulatus* var. *nevadensis* which he had described earlier from "near Truckee" (1893, p. 361).

Through the kindness of Dr. L. B. Smith at the Gray Herbarium, I have been able to examine the Lemmon and Ames collections referred to by Gray and they obviously represent a form of *Cirsium Breweri* (Gray) Jepson with stems, leaves, and involucres greenish and subglabrate, a form scarcely deserving nomenclatural recognition until the entire *Cirsium Breweri* complex is better understood.[1] Certainly with its glutinous-spotted and broader phyllaries it is not the same as the plant from Truckee and it seems likely that Greene would never have confused it with his Truckee plant had he seen the specimens cited by Gray. Since in his description of *Carduus inamoenus* Greene actually describes the Truckee specimens rather than those of Ames and Lemmon, and also since he states that his *Carduus undulatus* var. *nevadensis* is *Carduus inamoenus,* I believe that Greene's name should apply to the Truckee plant as typified by his own collections.

In Herb. Greene. two specimens collected by Greene represent the type of *Carduus inamoenus,* one from "near Truckee," the other from "east of Truckee or near that place," both dated August, 1883. An isotype has been seen in the Field Museum, designated as from the "Truckee Valley"; and, under the generic name *Cnicus,* it bears an unpublished specific name by which Greene had intended to honor H. W. Harkness, for a number of years president of the California Academy of Sciences. I have had the privilege of borrowing this specimen from the Field Museum for further study, and although the specimen agrees well with the diagnoses of Greene's variety and species for the most part, there are several details which should be examined critically.

In his description of *Carduus inamoenus,* Greene describes the plant as "2-3 ft. high, hoary-tomentose even in age. . . ." Judging from the thickness of that part of the main stem in Greene's specimen (nearly 2 cm. in diameter), it would seem that the plant might have been much taller, resembling

[1] The collections of Mrs. Ames and of Lemmon were compared with the specimens of *Cirsium Breweri* in Herb. Calif. Acad. Sci. and they were found to match almost exactly a collection by Heller from Butte Meadows, Butte County *(No. 11652).*

in habit tall specimens of *Cirsium Breweri*. Moreover, the plant is not "hoary-tomentose": the main stem is rather thinly floccose-arachnoid and the leaves are better described by Greene in his var. *nevadensis*, "green and glabrate above, hoary-arachnoid below. . . ." Comparing Greene's specimen with those of Mrs. Ames and of Lemmon described by Gray, I would say that the chief points of resemblance are in the habit and vesture.

The most serious discrepancy, however, in Greene's description of *Carduus inamoenus* is in the shape of the phyllaries which he describes as "ovate." In his description Greene is contrasting the phyllaries with those of *Carduus hydrophilus*, but a comparison of a specimen of the latter from the Suisun Marshes (*J. T. Howell No. 14590*) with the Truckee thistle discloses that whereas the phyllaries of the marsh plant are ovate-lanceolate to ovate, those of the Sierran plant vary from narrowly ovate-lanceolate or lanceolate on the outside to linear-lanceolate in the innermost. These narrow phyllaries, closely imbricated in 6 or 7 rows and "destitute of the glutinous ridge," constitute the chief character by which *Carduus inamoenus* differs from *Cirsium Breweri*.

Although *Carduus inamoenus* appears to be a recognizable entity, I do not believe that the specific name should be transferred to *Cirsium* until its relations and field occurrence are better understood. It seems likely that Greene's Truckee thistle has been derived from a cross between *Cirsium Breweri* and certain mid-Sierran forms related to *Cirsium triacanthum* Petrak (1917, p. 481). I have collected forms of both these thistles in the Truckee River Canyon east of Truckee and so it is not improbable that hybridization should occur in the region. The Truckee thistle, however, is not at all like a definite first generation hybrid between these two species which I discovered in Lassen County in 1940 in which the plant was more like the *triacanthum* parent. (Cf. discussion of *Cirsium triacanthum* below.)

C. "The Plant of Vasey's Collecting"

As Greene indicates in the original description of *Carduus inamoenus* (1897, p. 479), the name *Cnicus Breweri* var. *Vaseyi* Gray (1884, p. 404) should apply to "the plant of Vasey's collecting" from Mt. Tamalpais, Marin County, California, rather than to either of the other two elements included by Gray in his variety (cf. discussion of the "*Vaseyi* complex" under *Carduus inamoenus*). I believe that this typification of Gray's variety suggested by Greene should be followed, not only because it is part of the historical segregation of entities in Gray's var. *Vaseyi*, but it is also the logical disposition of a perplexing problem. Later workers, however, have not followed Greene in this interpretation but have preferred to regard the first-cited collections by Mrs. Ames and by Lemmon from the Sierra Nevada the type of *Cnicus Breweri* var. *Vaseyi*.[2]

2 It would seem certain, also, that Gray did not intend that the Sierran collections should typify his variety since the sheet on which the Ames and Lemmon specimens are mounted carries his annotation "Cnicus Breweri Gray fere var. Vaseyi." Obviously in writing "fere" Gray was contrasting these specimens with what he considered typical var. *Vaseyi*.

Heller (1904, p. 61), in applying that bothersome principle that a species should have as a specific epithet the oldest varietal or specific epithet applied to it, makes the combination *Carduus Vaseyi* and gives *Carduus inamoenus* Greene (1897) as a synonym. As I have pointed out in the discussion of *Carduus inamoenus*, the type of Greene's species is different from the Sierran element in Gray's var. *Vaseyi*, so Heller was in error considering *Carduus Vaseyi* and *Carduus inamoenus* synonymous.

In 1917, Petrak follows Heller's incorrect disposition of these entities and says the Sierran thistle described as *Carduus inamoenus* by Greene should receive (*erhalten*) the name *Cirsium Vaseyi* (1917, p. 455). Unfortunately Petrak had to depend entirely on Heller for his interpretation of Greene's *Carduus inamoenus* since it it obvious from this and other texts that he did not see Greene's important work on thistles in Flora Franciscana (cf. Petrak, p. 562 under *Carduus cymosus*). Because he regards the Tamalpais thistle without a name, Petrak describes it as *Cirsium montigenum* (1917, p. 454). In at least five places Petrak used the name *C.(irsium) Vaseyi* (1917, pp. 240, 242, 455, 458, and 459), but since it was published without proper references and was used without definite indication of purpose, I regard it as a *nomen nudum*.

Jepson (1925, p. 1165), after formally establishing the name *Cirsium Vaseyi*, refers the name to plants of the northern Sierra Nevada and northeastern California; but in giving the distribution as "dry or woody hillsides, 2000 to 4500 ft.: Siskiyou, Modoc and Butte Cos.," he omits Plumas and Sierra counties which should have been included from a historical consideration. These distributional data, together with the fact that the diagnosis does not agree with the plants of Lemmon and Mrs. Ames, have convinced me that Jepson applied his name to yet another Sierran thistle which will be discussed below under *Carduus cymosus* Greene. However that may be, it is my present purpose in determining the type of Gray's var. *Vaseyi* to follow Greene rather than Heller, Petrak, or Jepson with their erroneous applications of names and to consider Vasey's plant from Mt. Tamalpais the type of *Cnicus Breweri* var. *Vaseyi*.

Although Greene did much to elucidate Gray's complex var. *Vaseyi*, I have not found that he ever gave a name, specific or varietal, to the remarkable Tamalpais thistle, nor have I found Mt. Tamalpais or Marin County mentioned in his statements pertaining to the distribution of related thistles. Hence, contingent on my decision to regard "the plant of Vasey's collecting" as the type of *Cnicus Breweri* var. *Vaseyi* Gray, the earliest specific name properly applicable to the Tamalpais thistle is *Carduus Vaseyi* (Gray) Heller (1904, p. 61); and the proper combination in *Cirsium* I attribute to Jepson, since Petrak's use of the name is both improper and contradictory. Summarizing the nomenclature pertaining to the Tamalpais thistle as I see it, we have:

CIRSIUM VASEYI (Gray) Jepson, Man. Fl. Pl. Calif. 1165 (1925), as to name, not as to plants.

Cnicus Breweri Gray var. *Vaseyi* Gray, Synop. Fl. N. Amer. **1**, pt. 2: 404 (1884), as to Vasey's plant. *Carduus Vaseyi* (Gray) Heller, Muhl. **1**: 61 (1904). *Cirsium Vaseyi* (Gray) Petrak, Beih. Bot. Centralbl. **35**: 240, 242, etc. (1917), nomen nudum. *Cirsium montigenum* Petrak, op. cit., 454 (1917). *Cirsium Vaseyi* (Gray) Jepson var. *hydrophilum* (Greene) Jepson,[3] op. cit., 1165 (1925), in part.

Cirsium Vaseyi is apparently confined to the mountainous parts of Marin County adjacent to Mt. Tamalpais and in this area it is of rather common occurrence in wet meadows and springy places, frequently near serpentine. It is usually associated with *Zigadenus fontanus* Eastwood, which is rarely found beyond the Tamalpais area, and with *Stachys pycnantha* Benth., which is a more widely distributed but rather uncommon plant. (For further notes on the plant association in which *Cirsium Vaseyi* grows, see Howell, 1941, pp. 46, 47.) The thistle is biennial and the large rosettes of light green succulent leaves are a characteristic and conspicuous feature of Tamalpais meadows in the winter and spring.

The following collections of *Cirsium Vaseyi* are in Herb. Calif. Acad. Sci.: Mt. Tamalpais, *Eastwood No. 1556;* Azalea Flat, Mt. Tamalpais, *J. T. Howell No. 13897;* serpentine area near Bootjack, Mt. Tamalpais, *J. T. Howell No. 12657;* Potrero Meadow, Mt. Tamalpais, *J. T. Howell No. 17032;* Bolinas Road back of Liberty's, *Eastwood No. 3476.*

D. A Neglected Greenean Thistle

One of the chief accomplishments among the thistles at Notre Dame was the authentic determination of the Californian thistle, *Carduus cymosus* Greene (1897, p. 480). Although I had first collected the species on the north side of Mt. Diablo in 1931, it was not until 1938 when on a collecting expedition with Miss Eastwood in the Inner South Coast Ranges in Monterey County that the perennial character of the plant came to my attention and instigated a series of field and herbarium studies to establish its identity. Meanwhile in northern and northeastern California a series of collections of an obviously related plant was being assembled, and through specimens obtained from intermediate stations in Lake County, it was evident that the plants from northern California and from the South Coast Ranges might be the same. In several attempts at different times to fix the name of this northern plant I had variously determined it as *Cirsium Vaseyi, Carduus inamoenus, Cirsium Botrys,*[4] and even *Carduus venustus.* More recently this northern thistle has

3 In 1917, Petrak published this combination (p. 458) but I do not accept it since the specific name *Cirsium Vaseyi* had not been validly published at that time. Certainly a variety of a given species cannot be regarded as published if the species name has not been previously published.

4 The identity of *Cirsium Botrys* Petrak (1917, pp. 268, 483) itself is a problem. Petrak places it in his *Californica* group between *Cirsium triacanthum* Petrak and *Cirsium Howellii* Petrak. Of these two, the former is discussed fully in this section of my paper, and the latter is to be closely related to *Cirsium Breweri* (Gray) Jepson if my determination of a collection from southern Oregon (*M. E. Peck No. 3758,* Herb. Univ. Willamette.) is correct. It may be that *Cirsium Botrys* has originated by hybrid-

been found to be exactly *Cirsium triacanthum* Petrak (1917, p. 481); and with the examination of the thistle types at Notre Dame, the southern plant has been definitely determined *Carduus cymosus* Greene.

Little account has been taken of Greene's species in the literature. Not since Jepson included it as a sort of addendum in the first edition of his Flora of Western Middle California (1901, p. 507) has it been entered in our local floras by name, though it seems to form a part of Jepson's more recent entity *Cirsium occidentale* var. *Coulteri* (1925, p. 1167). Oddly enough, Petrak mentions *Carduus cymosus* only as a name, stating that he was unable to locate the original description (1917, p. 562).

Cirsium triacanthum was described from a single specimen collected by G. D. Butler near Yreka in Siskiyou County and so far as I can determine the name has not since been used in the literature of Californian botany. Jepson undoubtedly prepared his latest treatment of Californian thistles (1925, pp. 1161-1168) without reference to Petrak's revision (1917), and, while the plant described by Petrak as *Cirsium triacanthum* forms a large part if not all of Jepson's *Cirsium Vaseyi* (1925, p. 1165; see discussion of *Cnicus Breweri* var. *Vaseyi* above under *Carduus inamoenus* and *Cirsium Vaseyi*), it may be that the Sierran plants of Petrak's species also form a small part of Jepson's *Cirsium occidentale* var. *Coulteri* (1925, p. 1167).

Carduus cymosus and *Cirsium triacanthum* constitute a very distinct group among Californian thistles. The basal leaf-rosettes arise from buds which form on slender horizontal rootstocks, and although the erect aerial stems are strictly monocarpous, a stout perennial root-crown with several branches may eventually develop at or below the surface of the ground from one of the buds. As in so many thistles, the habit, vesture, foliage, and disposition of heads vary greatly, but the rather loosely imbricated slender phyllaries with shortly spinose tips enclosing the sordid whitish or buff flowers are very characteristic so that the heads look like the heads of no other western thistle. Since no marked morphological difference between the northern and southern plants has been detected, I choose to regard them the same species; and since Greene's name, which is the older, has never been published in *Cirsium,* I make the necessary transfer here:

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ization between *Cirsium triacanthum* and *Cirsium Breweri,* in spite of the fact that Petrak wrote on his annotation label "species distinctissima"!

The type of *Cirsium Botrys* (Herb. Calif. Acad. Sci.) consists of the inflorescence of a lanate-tomentose plant which carries a number of medium-sized heads on rather short mostly leafless branchlets. The phyllaries are lanceolate or lanceolate-ovate, subappressed, shortly spinose-tipped, and subglabrate, and the middle ones bear a narrowly oblong glutinous ridge. Certainly these technical characters place the plant between *Cirsium triacanthum* and *Cirsium Breweri.* Other plants resembling it have been seen from southern and middle Oregon, so a proper estimate of it can scarcely be reached until the possible interrelations between the two groups of thistles are known more fully throughout the region.

Cirsium cymosum (Greene) J. T. Howell, comb. nov.

Carduus cymosus Greene, Fl. Francis. 480 (1897). *Cirsium triacanthum* Petrak, Beih. Bot. Centralbl. **35**: 481 (1917). *Cirsium Vaseyi* Jepson, Man. Fl. Pl. Calif. 1165 (1925), as to diagnosis and distribution, not *Cnicus Breweri* var. *Vaseyi* Gray.

Concerning the relationship of *Cirsium triacanthum*, Petrak (1917, p. 482) states that it gives the impression of being a hybrid between a species of the *Cirsium californicum* group and *Cirsium remotifolium*. He treated it as a member of his "*Californica*-Gruppe" since he believed that it was much nearer to that group morphologically than to *Cirsium remotifolium*. To me, *Cirsium cymosum* seems quite obviously related to *Cirsium remotifolium* (Hook.) DC., another perennial species with underground rootstocks and with sordid whitish or buff flowers. In *Cirsium remotifolium*, however, the phyllaries are elongate and erect-spreading and the margins are frequently, but not always, more or less spinose-lacerate or spinose-dentate. The middle phyllaries of *Cirsium cymosum* usually bear a median elevated waxy or resinous line which may indicate a relation to *Cirsium undulatum*, but a similar ridge is also frequent in *Cirsium californicum* sens. lat.

The following collections of *Cirsium cymosum* from California have been studied in Herb. Calif. Acad. Sci. unless otherwise indicated.

SOUTH COAST RANGES: Walnut Creek, Contra Costa County, June 20, 1892, *Greene* (type, Herb. Greene.); north side of Mt. Diablo, Contra Costa County, *J. T. Howell No. 6478*; near Rock City, Mt. Diablo, Contra Costa County, *J. T. Howell No. 17039*; Tesla hills, Alameda County, *Eastwood & Howell No. 5802*; Patterson Pass, Alameda County, *Eastwood & Howell No. 5786, 5787*; Smith Creek, Mt. Hamilton, Santa Clara County, *Eastwood & Howell No. 9664*; Pacheco Pass, Merced County, *Eastwood & Howell No. 5332, J. T. Howell No. 13821*; Panoche Pass, San Benito County, *Eastwood & Howell No. 5214*; Mustang Grade, Monterey County, *Eastwood & Howell No. 5823*.

NORTH COAST RANGES: upper St. Helena Creek Canyon, Napa County, *J. T. Howell No. 15467*; Reiff P. O., Lake County, *J. T. Howell No. 14647*; Binkley Ranch, between Cobb Mt. and Adams Springs, Lake County, *Jussel No. 359*; 6 miles north of Lower Lake, *Eastwood & Howell No. 5586*; on road to Williams, eastern Lake County, *J. T. Howell No. 13143*; near Alder Springs, Glenn County, *Eastwood & Howell No. 9918*; Trinity River between Coffee and Eagle creeks, *Eastwood & Howell No. 4952*; Tangle Blue Creek, Trinity County, *J. T. Howell No. 13607*; Scott Mt. between Trinity and Siskiyou counties, *J. T. Howell No. 13649*.

NORTHERN CALIFORNIA and SIERRA NEVADA: Yreka, Siskiyou County, *C. D. Butler No. 1368* (Herb. Univ. Calif., type collection of *Cirsium triacanthum* Petrak); 5 miles north of Yreka, Siskiyou County, *Eastwood & Howell No. 1738*; 8 miles north of Weed, Siskiyou County, *Eastwood & Howell No. 2758*; between Igerna and Weed, Siskiyou County, *Heller in 1905*; Cantara, Siskiyou County, *Eastwood No. 12001*; Fandango Pass, Warner Mts., Modoc County, *J. T. Howell No. 12058, Eastwood & Howell No. 8154*; Cedar Pass, Warner Mts., Modoc County, *L. S. Rose No. 40560*; Parker Creek, 5200 ft., Modoc County, *Payne No. 329*; Fall River Mills, Shasta County, *Eastwood & Howell No. 7909*; Madeline Plain near Termo, Lassen County, *J. T. Howell No. 11908*; 5 miles east of McArthur, Lassen County, *Cantelow in 1940*; grade between Beckwith and Red Clover Valley, Plumas County, *Heller & Kennedy No. 8880*; dry hills, Butte County, *Austin in 1894* (Herb. Greene.)

OREGON (south central): 10 miles east of Lakeview, Lake County, *Peck No. 19600*

(Herb. Univ. Willamette.); 12 miles north of Paisley, Lake County, *Peck No. 20810*; 9 miles south of Summer Lake P. O., Lake County, *Peck No. 20801* (not typical in the elongate spines on phyllaries); "Yanex Reservation, S. E. Oregon," *Austin in 1893* (Herb. Greene.). On present-day maps is "Yainax Butte" near the Klamath Indian Reservation, Klamath County, and it may have been in that vicinity where Mrs. Austin made her collection.

A plant which is obviously a hybrid between *Cirsium cymosum* (*Eastwood & Howell No. 8307*) and *Cirsium Breweri* (*No. 8306*) was found on Willow Creek near Hayden Hill, Lassen County (*No. 8308*). In aspect the plant was more like *Cirsium cymosum* but it was more tomentose throughout and the flowers were pink.

Near Eldridge, 10 miles southeast of Fall River Mills, Lassen County, I collected a form much more arachnoid-woolly than usual (*J. T. Howell No. 12563*). Since it was growing with Greene's white-woolly Siskiyou thistle,[5] I suspect that it may represent a hybrid between that species and the thinly arachnoid *Cirsium cymosum*.

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5 **Cirsium Pastoris** J. T. Howell, nom. nov. *Carduus candidissimus* Greene, Proc. Acad. Nat. Sci. Philadel. **44**: 359 (1893). *Carduus occidentalis* Nutt. var. *candidissimus* (Greene) H. M. Hall, Univ. Calif. Publ. Bot. **3**: 240 (1907). *Cirsium occidentale* (Nutt.) Jepson subsp. *candidissimum* (Greene) Petrak, Beih. Bot. Centralbl. **35**: 496 (1917). *Cirsium occidentale* (Nutt.) Jepson var. *candidissimum* (Greene) Macbr., Contrib. Gray Herb., n. ser., **53**: 22 (1918). *Cirsium candidissimum* (Greene) Dav. & Mox., Fl. S. Calif. 438 (1923). Not *Cirsium candidissimum* Dammer, Gard. Chron. 1898, pt. 1, p. 161.

The type of this distinctive thistle was collected by Greene while he was pastor of the Episcopal Church in Yreka, Siskiyou County, in 1876. To Mr. R. C. Barneby I am grateful for the peculiarly appropriate specific epithet which he suggested during a discussion relative to renaming northern California's most spectacular thistle.

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SAN FRANCISCO, CALIFORNIA.

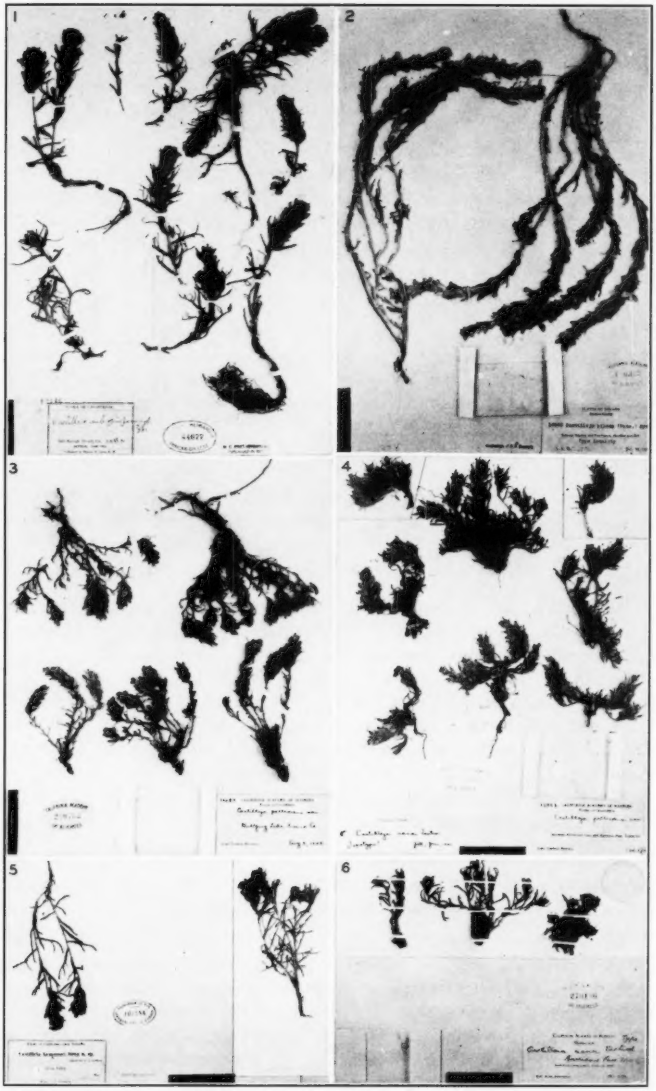
Some Alpine Castillejas of the High Sierra of California

Alice Eastwood

The *Castillejas* which form the subject of this study belong to the group intermediate between *Castilleja* and *Orthocarpus*, separated by the perennial habit of the former as against the annual habit of the latter. They are more closely related to *Castilleja pallescens* (Gray) Greenman (Coult. Bot. Gaz. 25:266. 1898) than to any other species though they seem to have been included in *C. pilosa* (Watson) Ryd. Mem. N. Y. Bot. Garden 1:361. 1900. In Dr. Gray's original description of *Orthocarpus pallescens* Silliman's Journ. 34 Ser. 2, 339. 1862, he included Torrey's *363* from Donner Lake 1866 (tips of bracts and corolla white) and Brewer's *2838* from high Sierra of California. In his later description of *Orthocarpus pallescens* Proc. Am. Acad. 7:384. 1867 he explains his perplexity as to the generic status of the group as follows:

> It is not easy to decide whether it should be ranked under *Orothocarpus* or *Castilleja*. The root is clearly perennial, as in no other *Orthocarpus*, and the lower lip is not as much triplicate as in some species of *Castilleja;* but in length it very nearly or quite equals the short galea, and its oblong lobes are about as long as the undivided portion. The coat of the seed appears to be cellular-favose, in the manner of *Castilleja;* but at maturity it forms an arilliform covering not much larger than the nucleus which lies loose within it. The species of *Orthocarpus* most like it is *O. attenuatus* Gray.

ORTHOCARPUS PILOSUS Watson, King's Report 231. 1871 under which these high mountain forms have been included was collected by Stretch in Washoe Valley, Nevada, and the type a poor specimen deposited in the Torrey Herbarium. When Rydberg transferred it to *Castilleja* Mem. N. Y. Bot. Gard. 1:361. 1900, his description was based on Heller's *10593*, collected between Washoe and Franktown, Nevada, the type locality, and an excellent specimen. A duplicate of this is in the herbarium of the California Academy of Sciences, a plant over 2 dm. tall, branching above, densely white hairy, quite unlike the low simple-stemmed high mountain plants, the subject of this study, the indument of which is glandular-puberulent and with viscid, fine wavy jointed hairs in the inflorescence, sometimes wanting on stems, rarely present on the leaves and this viscidity eventually turning the herbarium specimens black, though the appearance in fresh specimens is cinereous. All look alike though those from the highest elevations are low plants 2-5 cm. high, at lower elevations between 15-20 cm. high. The leaves are divaricate, the lowest generally linear, those above with 3-7 narrow linear divaricate divisions and generally a linear rachis. The inflorescence is generally capitate when young, later becoming spicate, dull colored, the color not generally evident in dried specimens but apparently not bright. While there is variation in the parts of the flowers, in all a brownish purple patch of color can be



1. *Castilleja ambigua* Jones, Type. — 2. *C. pilosa* (Wats.) Rydb. Type locality (Heller's No. 10593). — 3. *C. nana* Eastw. Topotype (Howell's No. 16087. *C. pallescens* var.) — 4. *C. nana* Eastw. Topotype. (Howell's No. 15857. *C. pallescens* var.). — 5. *C. Lemmoni* Gray. — 6. *C. nana* Eastw. Type.

seen on the corolla, generally near the throat but also in some extending up the back of the galea. The lower lip has three low rounded lobes, generally about 1 mm. in diameter. Several stems spring from a woody root.

The following have been segregated as species: *C. nana* Eastwood, Proc. Cal. Acad. Sci. 2, Ser. 3: 289-290. 1902. Type locality, Summit of Harrison's Pass, Tulare Co., Calif. *C. inconspicua* Nels. & Kenn., Proc. Biol. Soc. Wash. 19:30. 1906. Type locality, Mt. Rose, Washoe Co., Nev. *C. ambigua* Jones, Contr. West. Bot. 12:68. 1908. Type locality, Soda Springs, Nevada Co., Calif.

The parts of the flowers vary in so many ways that it does not seem possible with dried specimens to use them as specific or even varietal characters. This will be evident from the description of the floral organs of more than thirty specimens that have had one or more flowers examined under the dissecting microscope after having been soaked and dissected. Herbarium specimens are unsatisfactory because of the difficulty of examination and the limited number of flowers usually available, sometimes none, in each collection, so obvious characters have to be taken, such as the habit, character of indument and the general appearance that causes them all to look alike. Until airplanes become able to alight any place will it be possible to examine and compare specimens in one trip over the peaks, passes and other high altitudes from Sierra County in the north to Tulare County in the south.

The high mountain plants belonging to this group from the northern counties of California adjacent to the Oregon Boundary are not included. Their indument is quite different being a fine arachnoid tomentum indicating relationship with *C. arachnoidea* Greenman, Bot. Gaz. 53:510. 1912 under which they were included until Pennell segregated two species in Not. Nat. No. 74. 1941. Specimens from Mt. Shasta, Mt. Lassen and the high mountains of Siskiyou and Modoc counties are related to this group. *C. Payneae* Eastwood, Leafl. West. Bot. 2:245. 1940 from Warner Mt., Modoc Co., is one of them and all are related to *C. Lemmoni* Gray, Syn. Fl. II, 1:297. 1878, which has similar habit and indument.

The numbers of the specimens examined in the Herbarium of the California Academy of Sciences are the sheet numbers. Many specimens are from amateur collectors without numbers, but when there is a collector's number it is also given.

The following from Sierra County are doubtless to be included in *C. Lemmoni* Gray. They have similar indument and broad bracts barely surpassing the flowers. These bracts are similar to the leaves but the terminal division broadens to a truncate, obtuse, tridentate or apiculate apex. A brownish purple blotch is always present, generally at the base of the galea but in some extending upwards. The galea is finely puberulent on the back. Several stems arise from a woody root with the divaricate leaves, having linear divaricate divisions, turning black in drying. All are simple stemmed except *219160* and *28834* which branch near the top.

The following are from Sierra County: *219256* Salmon Lake, Dr. Kasper Pischel, calyx divisions surpassing corolla, galea equal to labium or slightly surpassing it. *219160* on dry rocky ridge, N.W. of Gold Lake, elev. 6900 ft., Lewis S. Rose No. *34298*, corolla scarcely surpassing the linear acute calyx divisions; galea and labium almost approximate. *28834* and *28833* mountains above Lake Center Camp, calyx divisions not surpassing the corolla, galea about reaching labium or slightly surpassing it.

The following are from places adjacent to what might be designated as the Lake Tahoe region where Nevada, Eldorado and Placer counties come together in California and adjacent Nevada on Mt. Rose: *28826* Ward's Pass, Eastwood, bracts with linear-acuminate divisions, slightly surpassing the flowers; calyx as long as or shorter than corolla, divisions unequal; galea surpassing labium, apex tridentate; two plants of this were collected one with all the leaves linear, the other with 3-5 linear divaricate divisions. *28829* along road from Fallen Leaf Lake to Glen Alpine, Eastwood, bracts irregular, slightly surpassing flowers, some with terminal divisions deltoid at apex, often with a tooth on one or both sides; calyx not quite equalling the corolla; galea acute, slightly surpassing the labium. *165664* Lake Gilmore, M. S. Jussel, bracts shorter or longer than the flowers, white-tipped, terminal division sometimes tridentate; calyx shorter or longer than corolla; galea about equalling labium or slightly surpassing it. *171388* trail to Desolation Valley above Glen Alpine, J. T. Howell *No. 1319;* bracts with terminal division often tridentate, the middle tooth longer and more acuminate, the tips of divisions surpassing the corolla or approximating it; galea tridentate at apex broad, surpassing labium. *28830* ridge east of Echo Lake, Eldorado Co., Heller No. *12142*, bracts yellowish, terminal division 3-cleft, acuminate, the tips surpassing corolla; galea tridentate, surpassing labium. *149277* Camp Sacramento, Eldorado Co., William Vortriede, bracts with terminal divisions with 2-3 short acute lobes slightly surpassing corolla; calyx about as long as corolla, divisions unequal; galea about equal to labium, apex tridentate or obtuse. *28943* amphitheatre on top of ridge, Madden Creek, Elizabeth Parsons Hawver: bracts scarcely surpassing the flowers, terminal division 2-3-cleft or dentate; calyx as long as or shorter than corolla; galea broad, tridentate at apex, the middle tooth broad and pointed, slightly surpassing labium.

CASTILLEJA AMBIGUA Jones, Soda Springs, Nevada Co., Calif. elev. 7000 ft. (these notes were made on the type which Dr. Munz loaned me from the M. E. Jones Herbarium at Pomona). Bracts surpassing the flowers, the middle division broader than the linear lateral, at apex deltoid and pointed; calyx divisions a little longer than the tube not surpassing the corolla; galea pointed surpassing the labium about 2 mm. The plant is robust with broad spikes. This description is added as the plant is allied to the Lake Tahoe series.

The specimens in this series become black in drying. The fine wavy hairs are sometimes wanting on the stems but always present on the inflorescence. The spikes show the pointed tips of the bracts slightly surpassing the flower. The stems are usually simple about 10-15 cm. high, several from a woody

root; a tendency to branch above is seen in the plants from Lake Gilmore and Camp Sacramento. In all the purplish spot is conspicuous at the throat of the corolla and in some extends upwards. They are all related to *C. inconspicua* owing to the viscidity of the fine wavy hairs.

This description of *Castilleja inconspicua* Nels. & Kennedy is from Heller's collection *No. 10347* from Mt. Rose. Bracts equal or a little shorter than flowers, terminal division 2 or 3 dentate or acuminate; calyx shorter than corolla; galea obtuse surpassing labium about 1 mm. In Heller's specimen the purplish color extends from the throat up the back of the galea; the spikes are broad as in Jones' *C. ambigua* and the plants from Lake Gilmore and Camp Sacramento.

The following are from alpine passes and peaks above 10,000 ft. elev. from Mt. Dana, Tuolumne County, to Harrisons Pass, Tulare County: these are all low tufted plants with spreading stems less than 10 cm. high, springing from a woody root. The specimens collected in the last 5 years all still show the cinereous indument. In older specimens including *C. nana* Eastwood, type, Harrisons Pass in 1899, Mono Pass in 1907 Eastwood collection and Kearsarge Pass collection of Mrs. Joseph Clemens in 1910 the plants have become black. *270186* Harrisons Pass, Eastwood, type, (specimen very young), bracts and calyx divisions linear acute surpassing the corolla; galea broad dark purplish, surpassed by divisions of labium. *28817* Harrisons Pass, Mrs. Marian L. Campbell (a meager specimen and older), divisions of bracts and calyx linear acute about equalling the corolla; galea broad, purplish near base, equal to labium. **278822* between Reflection Lake and Harrisons Pass, J. T. Howell *No. 15857,* divisions of bracts and calyx linear acute, shorter than the corolla; galea broad purplish at throat surpassing the labium 1 mm. *38428* Kearsarge Pass, Fresno Co., Mrs. Joseph Clemens, divisions of bracts and calyx linear acute, surpassing corolla; galea broad, purplish at base equal to labium. **280752* Bullfrog Lake at foot of Kearsarge Pass, J. T. Howell *No. 16087,* divisions of bracts and calyx linear acute surpassing corolla; galea with purplish spot at throat equalling the lower lip. *291256* Mono Pass, Fresno Co., J. T. Howell, *No. 16396,* divisions of bracts and calyx linear-acute, shorter than corolla; galea purplish at throat, acute, surpassing divisions of lower lip 2 mm. *28823* Mono Pass, Eastwood, the same as preceding. *265525* Mt. Dana, Tuolumne Co., J. T. Howell, *No. 14538;* divisions of bracts and calyx linear-acute, as long as or shorter than corolla; galea purplish at throat and above, obtuse, surpassing labium about 1 mm. *290720* Dusy Basin, Palisade Lakes, Fresno Co. elev. 10-12000 ft., Malcolm G. Smith; divisions of bracts and calyx linear acute, shorter than corolla; galea obtuse, purplish on throat, surpassing labium 1 mm. *202288* Pioneer Basin, Fresno Co., elev. 11000 ft., A. S. Crafts *No. 621;* bracts scarcely surpassing the corolla, terminal division generally tridentate broader than the linear acute lateral divisions; calyx about as long as corolla; galea obtuse, purple at throat and above equalling labium. This specimen is taller than all the preceding and more erect, glandular-

* Lower altitude from preceding collection.

puberulent and slightly hairy, becoming black. *269606* Rock Creek Lake Basin, Inyo Co. elev. 10800 ft., Frank W. Peirson collected in 1939 and said to be the same as his *7487* of 1931; divisions of bracts and calyx shorter than corolla; galea acute purplish at base, surpassing the labium.

The following are from lower elevations: *291802* near Garnet Lake, Madera Co. elev. 9700 ft., J. T. Howell, *No. 16763;* divisions of bracts and calyx linear acute not surpassing corolla; galea purple coarsely puberulent on back, purplish throughout, equal to labium, glandular puberulent with some spreading hairs. *291825* ridge northwest of San Joaquin Mt., Madera Co., J. T. Howell, *No. 16608;* bracts surpassing flowers, terminal broader than lateral, apex obtuse, acute or dentate, generally acute; calyx divisions linear acute unequal, the longest reaching the top of the galea; galea obtuse, purplish throughout, slightly surpassing labium; stems and leaves glandular puberulent and with some spreading hairs. *290936* near Thousand Island Lake, Madera Co., J. T. Howell, *No. 16706;* divisions of bracts and calyx linear acute slightly surpassing or equalling corolla; galea obtuse, purplish at base, surpassing labium 1 mm. This is a younger plant than the two preceding and grew on the north side of the mountain, in habit like the alpine plants at much greater elevations; stems and leaves with spreading hairs and glandular puberulent. *300145* Kaweah Gap, Tulare Co., J. T. Howell, *No. 17626;* linear acute divisions of bracts and calyx not surpassing the corolla; galea acute purplish throughout, surpassing labium, hairs only in spike. *300177* Timber Gap, Tulare Co., J. T. Howell, *No. 17284;* linear acute divisions of bracts and calyx scarcely surpassing corolla; galea purplish dorsally about as long as labium, viscid puberulent hairs on spike. *300809* Little Five Lakes Basin, Tulare Co., J. T. Howell, *No. 17400;* linear acute divisions of bracts and calyx shorter than corolla; galea purplish throughout, as long as labium, glandular puberulent, hairs only in spike. *271180* Sonora Pass Eastwood & Howell, *No. 7571;* divisions of bracts and calyx slightly surpassing the corolla or equalling it; galea acute at apex, purplish at throat surpassing the green labium 1 mm., glandular puberulent and hairy. *28828* Mt. Hoffman, Mariposa Co., Eastwood; divisions of bracts whitish, linear acute, terminal divisions sometimes trifid; divisions of calyx unequal some surpassing corolla, others shorter; galea acute at apex, purple at throat as long as or slightly surpassing labium; glandular puberulent and a little hairy. *265522* Upper Crabtree Meadow, Tulare Co. near foot of Mt. Whitney, Miss Jessie Saunders; bracts about as long as corolla, terminal divisions broader than the linear, acute lateral; corolla surpassing calyx; galea coarsely puberulent, purplish, obtuse, as long as the broad labium with obtuse divisions 1 mm. long and a little wider. *265523* Promontory at May Lake, Mariposa Co., Mrs. H. P. Bracelin, *No. 885;* bracts slightly surpassing the corolla, the terminal linear acute or broader than the lateral and 2-3-cleft or 2-3-toothed at apex; calyx as long as or shorter than corolla; galea coarsely puberulent, purple obtuse, not surpassing broad lower lip with short rounded divisions. *219172* White Mountains, Mono Co., Joseph Grinnell; bracts shorter than flowers, terminal divisions obtuse or 3-lobed at apex; calyx shorter than corolla; galea broad surpassing labium 2 mm., lobes of labium a

little over 1 mm. long obtuse. *269606* Rock Creek Lake Basin, Inyo Co., Frank W. Pearson; divisions of bracts and of calyx shorter than corolla; galea slightly puberulent, purplish at base, surpassing the labium about 1 mm.

From a comparison of all these specimens which I have examined, the relative position of bracts, calyx divisions, upper and lower lip of corolla with reference to each other is so variable and prevails irrespective of localities so that from the flowers and spikes it seems impossible to separate them even into varieties. The alpine plants from Harrisons Pass, type locality of *C. nana* Eastwood, Kearsarge Pass, Dusy Basin are less hairy on stems and leaves than specimens from Mono Pass and Mt. Dana. Those from Bullfrog Lake at the foot of Kearsarge Pass and Reflection Lake at the foot of Harrisons Pass are less tufted and taller plants with the divaricate, divided leaves more evident. The leaves in the plants at the highest elevations seem to be all linear entire except just below the inflorescence where they become bracts. The galea is dorsally glandular puberulent varying in density and in some under the lens seeming to be covered with very short gland-tipped hairs. I believe the calyx to be equally cleft but the difficulty of dissecting so as not to tear the parts makes this uncertain. It is a most puzzling group but probably not more so than others when comparisons can be made in the field as I have been able to in *C. latifolia* and *C. affinis* (Leafl. West. Bot. 1:235. 1936).

Through the kindness of Dr. H. L. Mason, Curator of the Herbarium, University of California, I have been able to see isotypes of *C. Lemmoni* Gray also Brewer's *No. 2838* from the high Sierra of California. The habit, foliage and pubescence of Brewer's specimen are more like those of *C. pilosa* (Watson) Ryd. which had not been described in 1861 and 1867 when Gray described *O. pallescens*.

To Dr. Munz also my sincere thanks are due for the loan of *C. ambigua* Jones.

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Key and Synopsis of the American Species of the Genus Chenopodium L.*

Paul Aellen and Theodor Just

Despite its great practical and theoretical interest, our knowledge of the genus Chenopodium L. is far from being complete. Many of its species are highly variable and have often been misunderstood. While the senior author's earlier contribution (Aellen 1929) was mainly concerned with a critical study of the nomenclature and distribution of all American forms, the present paper is designed to serve primarily as a means for identification.

As more material comes to light and all available collections can be studied, many forms may have to be added or reassigned, a desirable procedure should it simplify the present disposition of difficult groups. The distribution data are mostly those assembled by the senior author in the process of his revision of the whole genus in its world wide occurrence. Obviously many American records will have to be added in the future.

Since a complete list of chromosome numbers as found in the genus Chenopodium does not seem to be available in the literature, the following table was compiled as a basis for future studies, both taxonomic and cytological. Species not known to occur in America are also included. For details see Cooper 1935, Kjellmark 1934, Lorz 1937, Maude 1939-1940, Winge 1917, Woroshilov 1942, Wulff 1936.

TABLE 1. Chromosome numbers in the genus Chenopodium L.

Species	n	Author	n	Author
album	9	Winge	18	Cooper
album	9	Maude		
var. *Borbasii* f. *Bernburgense*	27	Kjellmark		
f *pseudo-Borbasii*	27	Kjellmark		
f. ad ssp. *diversifoliam*	27	Kjellmark		
var. (exot.)	27	Kjellmark		
amaranticolor	18	Wulff		
ambrosioides	18	Kjellmark		
ambrosioides	16	Lorz	16	Woroshilov
anthelminticum	32	Woroshilov		
Bonus Henricus	18	Winge	18	Wulff
capitatum	9	Kjellmark		
chilense	16	Woroshilov		
ficifolium	9	Kjellmark		
foetidum	9	Kjellmark		
glaucum	9	Wulff		
hybridum	9	Winge	18	Cooper
integrifolium	16	Woroshilov		
missouriense var. *Bushianum*	27	Kjellmark		

* Contribution from the Botanical Institute, University of Basel, Basel, Switzerland and the Greene and Nieuwland Herbaria, University of Notre Dame, Notre Dame, Ind.

murale	9	Winge		
nitrariaceum	18	Wulff		
opulifolium	18	Wulff		
polyspermum	9	Kjellmark		
pratericola	9	Kjellmark		
Probstii	27	Kjellmark		
Quinoa	18	Kjellmark	18	Wulff
rubrum	18	Kjellmark		
suffruticosum	16	Woroshilov		
virgatum	27	Kjellmark	9	Wulff
viride	9	Kjellmark		
Vulvaria	9	Winge		

No attempt has been made to correlate these numbers with the respective entities treated in the synopsis. The counts are apparently incomplete and show some discrepancies which may be the result of polysomaty, the existence of different chromosomal races, or the use of different taxonomic groups confused under the same name. At any rate, more exceptions to the euploid series of the Chenopodiaceae based by Lorz (1937) on x=9 (or 3?) are now on record than were known to him. It seems, therefore, that much more cytological information is needed, before taxonomic conclusions can be drawn from it.

Acknowledgment for reading the entire manuscript and for valuable suggestions is due Dr. Paul C. Standley, Herbarium, Field Museum, Chicago, Ill., and Mr. C. A. Weatherby, Gray Herbarium, Harvard University, Cambridge, Mass. Mr. V. C. Asmous, Arnold Arboretum, Harvard University, Jamaica Plain, Mass., kindly furnished an excellent translation from the Russian original of W. N. Woroshilov's "Revision des espéces de *Chenopodium* de la section *Ambrina* (Spach) Hook. fil.", parts of which are quoted in this paper.

Key to the Sections of the Genus Chenopodium L.

1. Plants lanuginose or glandular (rarely glabrous or subglabrous like *Ch. aristatum* L.), mostly aromatic.
   2. Seeds vertical; flowers in axillary glomerules, rarely in ebracteate panicles.
      3. Perianth reticulately veined, fused, 4-5-tipped.....Sect. I. *Roubieva*, p. 49.
      3. Perianth smooth, free almost to the base in the single American species.....Sect. II. *Orthosporum*, p. 50.
   2. Seeds mostly horizontal, occasionally vertical.
      3. Flowers in irregular glomerules. Inflorescence mostly spicate-paniculate.....Sect. III. *Ambrina*, p. 50.
      3. Flowers in loose, dichotomous cymes .....Sect. IV. *Botryoides*, p. 56.
         4. Plants with numerous glandular hairs .....Subsect. 1. *Botrys*, p. 56.
         4. Plants glabrous or subglabrous, with short glandular and vesiculose hairs .....Subsect. 2. *Teloxys*, p. 57.

1. Plants glabrous or bullate or (less commonly) glandular, but never lanuginose (pubescent).
   2. Seeds all vertical or partly vertical and horizontal.
      3. Perianth of terminal glomerulate flowers free almost to the base, 4-5-tipped, seeds horizontal; perianth of lateral glomerulate flowers partly fused, 3-tipped, seeds vertical ..... Sect. V. *Degenia*, p. 57.

3. Perianth of flowers with vertical seeds 3-5-tipped, free to the middle.
4. Perianth fleshy at maturity ..... Sect. VI. *Eublitum*, p. 59.
4. Perianth not fleshy.
5. Plants annual ..... Sect. VII. *Pseudoblitum*, p. 59.
5. Plants perennial.
6. Leaves pinnatifid or pinnately lobed. Glomerules bracteate..... Sect. VIII. *Thellungia*, p. 61.
6. Leaves triangular to spatulate, entire or dentate. Glomerules mostly ebracteate..... Sect. IX. *Agathophyton*, p. 61.
2. Seeds nearly always horizontal. Perianth 5-tipped, (rarely for lack of space) in dense glomerules with fewer tips and oblique or vertical seeds..... Sect. X. *Chenopodia*, p. 61.
3. Seeds smooth or nearly so..... Subsect. 1. *Lejosperma*, p. 61.
3. Seeds marked with grooves, ridges etc.
4. Seeds with regular surface markings in form of alveolar cells ..... Subsect. 2. *Cellulata*, p. 69.
4. Seeds with irregular surface markings.
5. Seeds with undulate ridges ..... Subsect. 3. *Undata*, p. 74.
5. Seeds with rough, suborbicular or elongate grooves and lacerated edges..... Subsect. 4. *Grossefoveata*, p. 75.

Synopsis of the Sections, Species and Subspecific Entities of the Genus Chenopodium L.

Sect. I. ROUBIEVA Rouy in Rouy et Foucaud, Fl. France **12**, 2:53. 1910. Moquin in Ann. sci. nat., 2e sér., **1**:292. 1834—as genus.

Perianth fused, saccate, 4-5-tipped, reticulate. Seeds vertical. Flowers in axillary glomerules.

KEY TO SECTION ROUBIEVA

1. Perianth ovoid-globose, 1-2.5 (-3) mm. long, sessile (or nearly so). Seed 0.75 (-1) mm. in diam. Most leaves narrowly pinnatifid ..... *Ch. multifidum*
2. Leaf segments narrow. Perianth sessile.
3. Perianth 1-2 mm. long. Seed 0.75 mm. in diam. ..... f. *typicum*
3. Perianth 2.5-3 mm. long; oblong-ovate (as in *Ch. Haumani* but sessile). Seed 0.75-1 mm. in diam. ..... f. *intermedium*
2. Leaf segments broader or leaves undivided. Perianth pedicillate.
3. Leaf segments broader ..... f. *latisectum*
3. Uppermost leaves spatulate, entire, 6-7 mm. long ..... f. *spathulatum*
1. Perianth oblong-ovate, 2.5-4 mm. long, pedicel 1-2 mm. long. Seed 1 mm. in diam. Leaves mostly broader, pinnately lobed or at best sinuate-dentate ..... *Ch. Haumani*

1. CHENOPODIUM MULTIFIDUM L. Spec. Pl. 220. 1753.—*Roubieva multifida* (L.) Moq. in Ann. sci. nat., 2e sér., **1**:292. 1834.

South America, Juan Fernandez. Introduced from New York to Alabama, California.

f. **typicum** Aellen, f. nov.—Segmenta foliorum angusta.

f. LATISECTUM Bonte et Aellen in Verh. Naturf. Ges. Basel **41**:94. 1930.

f. **spathulatum** Aellen, f. nov.—Folia suprema spatuliformia, integerrima, 6-7 mm. longa.

f. **intermedium** Aellen, f. nov.—Segmenta foliorum angusta. Perianthium 2.5-3 mm. longum, oblongo-ovale. Semen 0.75-1 mm. in diam. latum.

2. CHENOPODIUM HAUMANI Ulbrich in Engl. u. Prantl, Natürl. Pfl.-Fam., ed. 2, **16c**:491. 1934.—*Chenopodium bonariense* (Hook. f.) Hauman et Irigoyen—not Tenore.

Uruguay, Argentina.

Sect. II. ORTHOSPORUM R. Br., Prodr. Fl. Nov. Holl. **1**:407. 1810.

Perianth tips five, partly separated, smooth or with appendages. Seeds vertical. Flowers in axillary glomerules. Only one species in America.

3. CHENOPODIUM PUMILIO R. Br., Prodr. **1**:407. 1810.—*Ch. carinatum* of authors, not R. Br.; see Aellen, Verh. Naturf. Ges. Basel **44**(1):308-318. 1933.

Plants glandular. Leaves pinnatifid or dentate. Perianth tips oblong, narrow, arched, without appendages and keel, fused only at the base.

Australia. Introduced in Massachusetts, New Jersey, District of Columbia, Missouri, Texas, northern California.

Sect. III. AMBRINA (Spach) Hook. f. in Benth. et Hook., Gen. Pl. **3**:51. 1880.—Spach Hist. Nat. **5**:295. 1836—as genus. Beck in Rchb. Icon. xxiv: 118, 1908—for a section of the genus *Blitum*.

Perianth (4-)5-tipped, fused to about the middle, glabrous or puberulent. Seed normally horizontal, occasionally vertical. Inflorescence usually spicate-paniculate. Represented by a single but highly polymorphic species.

KEY TO SECTION AMBRINA

(Key to the subspecific entities of *Chenopodium ambrosioides* L.)

1. Perianth often rugose, carinate when mature (if strongly carinate, the perianth is stellate). Inflorescence almost ebracteate. Leaves irregularly laciniate-dentate or pinnatifid.
   2. Leaves irregularly laciniate-dentate. Perianth distinctly rugose .....ssp. *Venturii*
   2. Leaves pinnatifid, the segments mostly entire, acuminate. Perianth carinate (smooth, when young?) .....ssp. *Burkartii*
1. Keel of perianth segments small, rounded or absent. Inflorescence bracteate or, when ebracteate, leaves small, regularly and symmetrically dentate.
   2. Leaves ovate-spatulate, regularly sinuate-dentate. Inflorescence a terminal and ebracteate panicle. Glomerules ebracteate .....ssp. *retusum*
   2. Leaves acute (rarely obtuse), mostly acute-dentate or irregularly repand-dentate or sinuately lobed. Inflorescence and glomerules mostly bracteate.
      3. Leaves mostly narrow and laciniate-serrate or rarely ovate-elliptical and then sinuately lobed. Inflorescence ebracteate or nearly so. Seed with shallow depressions (rarely also with undulate lines) .....ssp. *chilense*
      4. Leaves oblong-ovate to lanceolate, acute .....var. *eu-chilense*

5. Bracts definitely longer than glomerules.
6. Leaves ovate-lanceolate to broadly lanceolate; teeth usually dentate ..... f. *normale*
6. Leaves narrower, lanceolate to linear, dentate ..... f. *angustatum*
5. Bracts small or absent ..... f. *denudatum*
4. Leaves rounded-ovate, with broad, lobe-like, dentate teeth, acute ..... var. *andicola*
3. Leaves mostly oblong-elliptical to broadly lanceolate, irregularly repand-dentate to entire, the larger ones sinuately lobed. Inflorescence bracteate. Seed almost smooth, with undulate lines ..... ssp. *eu-ambrosioides*
4. Glomerules ebracteate throughout inflorescence ..... var. *anthelminticum*
4. Glomerules bracteate.
5. Whole plant more or less lanuginose ..... var. *suffruticosum*
5. Plant almost glabrous (except glandular hairs) or sparsely lanuginose ..... var. *typicum* (with seven forms)

4. CHENOPODIUM AMBROSIOIDES L., Spec. Pl. 219. 1753.

ssp. **Venturii** Aellen, ssp. nov.

Folia (media) ad 6 cm. longa, ad 2 cm. lata, magnopere irregularia et profunde laciniato-dentata aut sinuato-dentata. Inflorescentia paene terminalis, breviramosa, aphylla. Glomeruli aphylli, catenulati. Perianthium ± carinatum, maturate saepe stellatum, albescens, spongiosum, venoso-rugosum. Carina gibbosa. Pericarpium ± liberum. Semen horizontale vel verticale. Corium seminis ± leve, paucis lineis anguineis praeditum.

Argentina: Tucuman, 2 Cuestas, 2400 m., 1926, S. Venturi no. 4435.

ssp. BURKARTII Aellen in Fedde Rep. spec. nov. **26**:37. 1929.

Argentina, Brazil?

ssp. RETUSUM Aellen in Fedde Rep. spec. nov. **26**:38. 1929.—*Ambrina retusa* Juss. ex Moq. Chenop. enum. 38. 1840.—*Chenopodium ovatum* Moq. in DC. Prodr. **13**(2):73. 1849.

Argentina, Brazil, Uruguay.

ssp. CHILENSE Aellen in Fedde Rep. spec. nov. **26**:36. 1929.—*Ch. chilense* Schrader, Ind. Sem. Hort. Gott. **1832**:2. 1832, not of Pers. 1805.—*Ch. vagans* Standley in N. Am. Fl. **21**:26. 1916.

var. EU-CHILENSE Aellen in Fedde Rep. spec. nov. **26**:36. 1929.

f. **normale** Aellen, f. nov.—Folia ovato-lanceolata ad late lanceolata, dentibus serratis.

Chile, Bolivia. Introduced in northern California.

f. ANGUSTATUM (Moq.) Aellen in Fedde Rep. spec. nov. **26**:36. 1929.—*Ch. chilense* var. *angustifolium* Moq. in DC. Prodr. **13**(2):74. 1849.

Chile, Argentina.

f. DENUDATUM (Phil.) Aellen in Fedde Rep. spec. nov. **26**:36. 1929.—*Ambrina denudata* Phil. in Linnaea **29**:37. 1856.

Chile, Brazil. Introduced in northern California.

var. ANDICOLA (Phil.) Aellen in Fedde Rep. spec. nov. **26**:37. 1929. —*Ambrina andicola* Phil. in Anal. Univ. Sant. **91**:442. 1895.—*Chenopodium querciforme* Murr in Mag. Bot. Lap. **3**:37. 1904.

Chile, Peru, Bolivia.

ssp. EU-AMBROSIOIDES Aellen in Fedde Rep. spec. nov. **26**:34. 1929.

var. ANTHELMINTICUM (L.) Aellen in Fedde Rep. spec. nov. **26**:35. 1929.—*Ch. anthelminticum* L. Spec. Pl. 320. 1753.

Missouri, Texas. Bermuda, Argentina, Brazil.

var. SUFFRUTICOSUM (Willd.) Aellen in Fedde Rep. spec. nov. **26**:35. 1929.—*Ch. suffruticosum* Willd. Enum. pl. hort. berol. **1**:290. 1809.

var. TYPICUM (Speg.) Aellen in Fedde Rep. spec. nov. **26**:34. 1929. —*Ch. ambrosioides a) typica* Speg. in Anal. Mus. Nac. B. Aires, 2. ser., **4**:137. 1902.

Central and southern N. America, Central and South America.

f. SPATHULATUM (Sieber) Aellen in Fedde Rep. spec. nov. **26**:35. 1929—*Ch. spathulatum* Sieber, Fl. Martin. 92. 1825.—Bracts large and spatulate.

f. GENUINUM (Willk.) Aellen in Fedde Rep. spec. nov. **26**:34. 1929.—*Ch. ambrosioides* L. var. *genuinum* Willk. in Willk. et Lange, Prodr. Fl. Hisp. **1**:271. 1861.—Bracts little, lanceolate or linear, leaf-blades oblong-elliptical to broadly lanceolate.

f. ANGUSTIFOLIUM (Moq.) Aellen in Verh. Naturf. Ges. Basel **41**:96. 1930.—*Ch. ambrosioides* L. var. *angustifolium* Moq. in DC. Prodr. **13**(2):73. 1849.—Leaf-blades narrow, lanceolate, and denticulate.

f. DENTATUM (Fenzl) Aellen in Verh. Naturf. Ges. Basel **41**: 96. 1930.—*Ch. ambrosioides* L. var. *dentata* Fenzl in Mart. Fl. Bras. **5**(1): 145. 1864.—Leaf-blades almost serrate-denticulate.

f. **integrifolium** (Fenzl) Aellen, comb. nov.—*Ch. ambrosioides* L. var. *integrifolium* Fenzl in Mart. Fl. Bras. **5**(1): 146. 1864.—Leaf-blades slightly dentate or entire.

f. **rotundatum** Aellen, f. nov.—Folia orbiculato-ovata.

f. **pinnatifidum** (Willk.) Aellen, comb. nov.—*Ch. ambrosioides* L. var. *pinnatifidum* Willk. in Willk. et Lange, Prodr. Fl. Hisp. **1**:271. 1861.—Leaf-blades almost pinnatifid.

The treatment of all forms belonging to Section Ambrina adopted in this synopsis differs widely from that proposed by Woroshilov (1942). *Chenopodium ambrosioides* L. is here regarded as a highly polymorphic species but is broken up by Woroshilov into twelve species with several subspecies and varie-

ties. One of these species (*Ch. integrifolium* Worosh.) and two subspecies (*Ch. integrifolium* ssp. *ramosissimum* and *Ch. suffruticosum* ssp. *remotum*) are described as new.

Woroshilov bases his disposition of these species and subspecific entities on the customary study of herbarium material, published information and, as far as possible, on data obtained from transplants, cytological analysis, chemical behavior, and geographical distribution. The following enumeration includes the entities known to occur in North and South America, nearly all of which appear in synonymy in the synopsis, and one species from Tristan da Cunha.

1. *Ch. spathulatum* Sieber.
2. *Ch. integrifolium* Worosh. with ssp. *ramosissimum* Worosh.
3. *Ch. ambrosioides* L. with var. *pinnatifida* Willk.
4. *Ch. suffruticosum* Willd. with ssp. *remotum* Worosh.
5. *Ch. tomentosum* Pet.— Thou.
6. *Ch. chilense* Schrad. with var. *angustifolium* Moq., var. *denudata* (Phil.) Reiche, and var. *incisa* (Phil.) Reiche.
7. *Ch. andicola* (Phil.) Reiche.
8. *Ch. Venturii* Aellen. See synopsis for diagnosis of *Ch. ambrosioides* L. ssp. *Venturii* Aellen, ssp. nov. Woroshilov based the transfer of this unpublished name to stat. nov. on herbarium material from the Herbarium P. Aellen.
9. *Ch. querciforme* Murr with var. *minus* Murr.
10. *Ch. anthelminticum* L.
11. *Ch. retusum* Juss.
12. *Ch. Burkartii* (Aellen) Worosh.

In addition to having the highest chromosome number (2n=64) *Ch. anthelminticum* L. is remarkable also, because it takes 145 days until the first flowers appear, whereas other species (*Ch. chilense* Schrad., *Ch. suffruticosum* Willd., *Ch. ambrosioides* L. and *Ch. integrifolium* Worosh.) require only 65-75 days. *Ch. suffruticosum* Willd. ssp. *remotum* Worosh. requires as many as 180 days to flower, although the typical species reaches that stage in 70 days. Differences in the time required for fruiting were also studied as were the yield of dry fruits with perianths in various parts of USSR (see Table 1 in Woroshilov 1942). *Ch. suffruticosum* Willd. gives the best yield (3.5 tons per ha).

Chemical analysis of all species investigated disclosed interesting and taxonomically valuable information. Although *Ch. ambrosioides* L. and *Ch. integrifolium* Worosh. look very much alike, they differ definitely in their volatile oil content. The former species contains at least 70 per cent ascaridol in its volatile oil, whereas the latter has only about 35 per cent (see Table 2 in Woroshilov 1942 for additional data).

In view of the general inaccessibility of Woroshilov's revision, the Latin descriptions of his new species and subspecies are here reprinted together with his Russian ones as translated by Mr. V. C. Asmous. The illustration of *Ch. integrifolium* Worosh. is reproduced from the original one.

Chenopodium integrifolium Worosh. sp. nov.

Chenopodium integrifolium Worosh. sp. nov. 'Mar' tsel'nolistnaia'. Caulis erectus, subglaber, ramosus, 30-80 cm. altus. Rami erecti. Folia tenuia, lanceolata vel obovato-lanceolata, integerrima vel subdentata, 4-8 cm. longa; floraria 1-2 cm. longa, acuta. Ramuli flloriferi dense foliati, abrupte glomerulati. Perianthium fructiferum suborbiculatum, apicem obtusum; lobis non carinatis. Semina .5 mm diametro.

Differt ab *Ch. spathulato* Sieber foliis floralibus acutis, non spathulatis; ab *Ch. ambrosioide* L. ramis erectis, foliis caulinis integerrimis vel subdentatis; foliis floralibus majoribus.

Area geogr. Europa australis, America media et borealis, Africa, Australia.

Typus. Hungaria. Kalocsa in pago Fokto, 17 ix 1875, leg. S. I. Menyharth, in Herb. Inst. Bot. Acad. Sci. URSS.

Stems 30-80 cm. high, subglabrous with erect branches. Leaves lanceolate or obovate-lanceolate, 4-8 cm. long, tapering towards both ends, acute at the apex, thin, mostly entire, rarely subdentate. At maturity most leaves fallen. Glomerules on the main stem almost to its base. Glomerules on the ultimate branchlets of the inflorescence interrupted, moniliform, subtending bracts large (1-2 cm. long), acute, broadly linear or lanceolate, 3-5 times longer than glomerules. Sometimes short (.5-3 cm. long) branchlets replace the glomerules. Perianth in fruit suborbicular, small, .75-1.0 mm. diam. subglobular, rounded on the apex, lobes not keeled. Seeds small, .5 mm. in diam.

Geogr. range. This species is widely distributed in southern Europe (Spain, Portugal, Italy, France, Greece, Austria, Hungary), Central America (Mexico, Guatemala); disjunct areas in North America (Missouri, New York, California), Africa, Australia. Described from Hungary. Type in Leningrad.

Subsp. ramosissimum Worosh. subsp. nov.—*Chenopodium ambrosioides* L. β *angustifolium* et *Ch. spathulatum* Sieber γ *angustifolium* Moq. in DC. Prodr. Syst. Nat. xiii, pt. 2 (1849) 73; ? *Ch. ambrosioides* L. γ *comosa* et ε *angustifolium* Willk. in Willk. et Lange, Prodr. Fl. Hisp. i (1861) 271.

Ramis adscendentibus; caulibus apicem et ramulis longis flexuosis; foliis tenuibus, integerrimis lanceolatis vel sublinearibus (var. *angustifolium* Moq.), floraribus longis, acutis.

Area geogr. Africa, Asia australis, America australis.

Typus. Central Madagascar, Maroharona pr. Tananarivo, 14 vi 1880, leg. I. M. Hildebrand; in Herb. Inst. Bot. Acad. Sci. URSS.

Differs from the species in the ascendent lower branches of the stem and in thin, flexuose ends of the stems and branches.

Geogr. range. Africa (Madagascar, Madeira, Capland), southern Asia (eastern India, French Indochina, Java, Philippines), South America (Brazil). Described from Madagascar. Type in Leningrad.

Chenopodium suffruticosum Willd.

Subsp. remotum Worosh. subsp. nov.

Serotinum. Caulis ad 150 cm. altus, apicem dense tomentosus. Ramuli floriferi abbreviati, tenui, valde abrupti (glomerulis remotis), foliacei. Folia floralia magna, ad 2 cm. longa.

Area geogr. America australis, Australia.

Typus. Uruguay, departamento Montevideo, Atahualpa, Casavelle vi 1926, leg. Herter; in Herb. Inst. Bot. Acad. Sci. URSS.

Very late flowering, tall plant with dense tomentose pubescence on the ends of stems and branches. Distinguished by abbreviated, slender, interrupted, foliaceous branchlets of the inflorescence. Bracts large, up to 2 cm. long.

Geogr. range. South America (Uruguay, Chile, Brazil), Australia. Described from Uruguay. Type in Leningrad.

Sect. IV. BOTRYOIDES C. A. Meyer in Ledebour, Fl. Alt. 1:410. 1829 in part.—*Botrydium* Spach, Hist. Nat. 5:298. 1836 as genus, in part.—*Botryois* Moq. in DC. Prodr. 13(2):72. 1849 as section, in part.

Flowers in loose, dichotomous cymes.

Subsect. 1. BOTRYS (Koch) Aellen et Iljin in Fl. USSR. 6:46. 1936.—*Botrys* Koch, Syn. Fl. Germ. Helv. ed. 1:607. 1837.

Plants (densely) glandular-pubescent.

KEY TO SUBSECTION BOTRYS

1. Keel of perianth tips smooth, inconspicuous, and glandular-pubescent.
   2. Leaves deeply 1-2-pinnatifid, with linear segments ..... 5. *Ch. dissectum*
   2. Leaves sinuate-pinnatifid, with broad segments ..... 6. *Ch. Botrys*
1. Keel of perianth tips tuberculate.
   2. Keel usually with several tubercles and a strong ridge ..... 7. *Ch. foetidum*
   2. Keel with one tubercle in distal part ..... 8. *Ch. graveolens*

5. CHENOPODIUM DISSECTUM (Moq.) Standley in N. Am. Fl. 21:26. 1916.—*Ch. bipinnatifidum* Moric. ex Moq. in DC. Prodr. 13(2):76. 1849.—*Ambrina dissecta* Moq. Chenop. enum. 38. 1840.

Mexico.

6. CHENOPODIUM BOTRYS L. Spec. Pl. 219. 1753.

Distributed throughout the United States and Canada.

7. CHENOPODIUM FOETIDUM Schrad. in Magaz. Ges. Naturf. Freunde Berlin: 79. 1808.—*Ch. Schraderianum* Schult. Syst. veg. 6:260. 1820.

American records uncertain.

8. CHENOPODIUM GRAVEOLENS Willd. Enum. pl. hort. berol. 1:290. 1809. Aellen in Verh. Naturf. Ges. Basel 41:105. 1930.—*Ch. incisum* Poir. in Lam. Encycl. méth. Suppl. 1:392. 1810.—*Ch. effusum* Martens et Galeotti in Bull. Acad. Brux. 10(1):346. 1843.—*Ambrina incisa* Moq. Chenop. enum. 36.1840. —*Teloxys cornuta* Torrey Pac. R.R. Rep. 4:129. 1857.—*Chenopodium cornutum* Benth. et Hook. Gen. Pl. 3:51. 1880; S. Wats. Bot. Calif. 2:482. 1880. —*Teloxys aristata* Moq. in DC. Prodr. 13(2)59. 1849, in part, not *Ch. aristatum* L.

var. BANGII (Murr) Aellen in Verh. Naturf. Ges. Basel 41:107. 1930.—*Ch. incisum* Poir. var. *Bangii* Murr in Bull. Herb. Boiss., 2e sér., 4:991. 1904.—*Ch. rigidum* Lingelsheim in Fedde Rep. spec. nov. 7:241. 1909.—*Ch. foetidum* and *Ch. Botrys* in part of South American authors, neither Schrad. nor L.—*Teloxys Mandoni* S. Wats. in Proc. Am. Acad. 9:91. 1874.—*Chenopodium Mandoni* Aellen in Fedde Rep. spec. nov. 26:160. 1929.—Plant mostly erect, stiff, with few branches. Leaves elliptic, sinuate-dentate, tip not aristate.

Bolivia, Peru, Argentina.

f. ROTUNDIFOLIUM Aellen in Verh. Naturf. Ges. Basel 41:108. 1930.—*Ch. incisum* var. *Bangii* f. *rotundifolium* Aellen in Fedde Rep. spec.

nov. 26:40. 1929.—Leaves rotund, slightly sinuate-dentate, the upper ones entire.

f. PUMILUM (Kurtz) Aellen in Verh. Naturf. Ges. Basel 41: 108. 1930.—*Ch. foetidum* f. *pumilum* Kurtz in Fries, Flora nördl. Argent. 156. 1905.—*Ch. incisum* var. *Bangii* f. *pumilum* Aellen in Fedde Rep. spec. nov. 26:40. 1929.—Plant small, delicate.

var. MEXICANUM Aellen in Verh. Naturf. Ges. Basel 41:108. 1930. —*Ch. incisum* var. *mexicanum* Aellen in Fedde Rep. spec. nov. 26:40. 1929. —*Ch. graveolens* Willd. in the narrower sense.—Leaves ovate, pinnately lobed, with long aristate tip.

Mexico.

var. NEOMEXICANUM Aellen in Verh. Naturf. Ges. Basel 41:108. 1930.—*Ch. incisum* var. *neomexicanum* Aellen in Fedde Rep. spec. nov. 26: 40. 1929.—Plants profusely branched. Leaves pinnate with narrow segments, not noticeably aristate.

Mexico, New Mexico, Arizona.

f. RUBELLUM Aellen in Verh. Naturf. Ges. Basel 41:108. 1930. *Ch. incisum* var. *neomexicanum* f. *rubellum* Aellen in Fedde Rep. spec. nov. 26:40. 1929.—Plant turning red.

Subsect. 2. TELOXYS (Moq.) Aellen et Iljin in Fl. URSS. 6:47. 1936.—*Teloxys* Moq. in Ann. sci. nat., 2e sér., 1:286. 1834.

Plants almost glabrous with short vesiculose or glandular hairs.

9. CHENOPODIUM ARISTATUM L. Spec. Pl. 221. 1753.

American records of this northern and northeastern Asiatic species uncertain.

Sect. V. DEGENIA Aellen in Magyar Bot. Lap. 25:56. 1926 (1927).

Terminal flowers of glomerules with free, 3-5-lobate perianth and horizontal seeds. Lateral flowers with fused, 3-tipped perianth and vertical seeds.

KEY TO SECTION DEGENIA

1. Plant delicate, with long branches. Leaves with long petioles, triangular to deltoid-ovate, entire to slightly three-lobed. Flowers in small, bracteate glomerules ..... 10. *Ch. frigidum*
1. Plants robust. Leaves large, up to 10 cm. long and wide, broadly triangular to deltoid, sharply sinuate-dentate or with one obtuse lateral tooth and then almost entire. Flowers in axillary (more or less cymose) or subterminal (paniculate) inflorescences.
   2. Plant glabrous or glabrescent ..... 11. *Ch. chenopodioides*
      3. Plant prostrate. Leaves usually entire or with a single obtuse lateral tooth, rounded-triangular ..... var. *Degenianum*
      3. Plant erect. Leaves more or less triangular, deeply sinuate-dentate, often lobed ..... var. *Lengyelianum*
   2. Plant copiously farinose, especially on the lower sides of leaves. Leaves petiolate, triangular-rhombic, sharply sinuate-dentate ..... 12. *Ch. macrospermum*
      3. Leaves and stem thick. Plant compact, prostrate. Glomerules axillary, not terminal in a panicle. Seed large, 1.25-1.5 mm. ..... ssp. *crassicaule*

3. Plant erect, up to 50 cm. high. Glomerules terminal in bracteate panicles. Seed 0.75-1 mm. in diam. ..... ssp. *halophilum*

10. CHENOPODIUM FRIGIDUM Phil. Flor. atac. no. 332. 1860; Reiche Fl. Chil. **6**(1):154. 1911.—*Ch. hypsophilum* Hauman in Anal. Soc. Cient. Arg. **86**:250. 1918.

Chile, Argentina.

11. CHENOPODIUM CHENOPODIOIDES (L.) Aellen in Ostenia :98. 1933.—*Blitum chenopodioides* L. Mant. pl. **2**:170. 1771.—*Ch. crassifolium* Hornem. Hort. Hafn. 254. 1813; Aellen in Magyar Bot. Lap. **25**:55. 1926 (1927).—*Ch. rubrum* and *humile* of North American authors, not of L. or Hook.

var. **Degenianum** Aellen, comb. nov.—*Ch. crassifolium* Hornem. var. *Degenianum* Aellen in Magyar Bot. Lap. **25**:58. 1926 (1927).

Washington, Nevada, California.

var. **Lengyelianum** Aellen comb. nov.—*Ch. crassifolium* Hornem. var. *Lengyelianum* Aellen l.c. :57.

Washington, Oregon, Utah, Nebraska.

12. CHENOPODIUM MACROSPERMUM Hook. f. Fl. Antarct. **2**:341. 1847.

ssp. CRASSICAULE (Moq.) Aellen in Fedde Rep. spec. nov. **26**:42. 1929. *Blitum rubrum* (L.) Rchb. var. *crassicaule* Moq. in DC. Prodr. **13**(2):84. 1849.—*Blitum rubrum* (L.) Rchb. var. *macrosperma* Speg. in Anal. Mus. Nac. B. Aires, 2. ser., **4**:141. 1902.—*Ch. macrospermum* Hook. f., s. str.

Falkland Islands, Tierra del Fuego.

ssp. HALOPHILUM (Phil.) Aellen in Fedde Rep. spec. nov. **26**:42. 1929.—*Ch. halophilum* Phil. in Anal. Univ. Sant. **18**:67. 1861.—*Ch. murale* var. *farinosum* S. Wats. in Proc. Amer. Acad. **9**:97. 1874.—*Ch. farinosum* Standley in N. Am. Fl. **21**:28. 1916.—*Chenopodium macrospermum* var. *halophilum* (Phil.) Standley in Field Mus. Nat. Hist. Bot. **11**:118. 1931.—*Chenopodium* and *Blitum rubrum* of South American authors, not of L.—Variable.

North Carolina, California, Mexico, Bolivia, Chile, Paraguay, Uruguay, Argentina.

f. SUBVIRIDE Thellung et Aellen in Fedde Rep. spec. nov. **26**:43. 1929.—*Blitum rubrum* var. *vulgaris* Speg. in Anal. Mus. Nac. B. Aires, 2e sér., **4**:141. 1902, not Moquin.—*Ch. rubrum* var. *vulgaris* Hauman et Irigoyen in Anal. Mus. Nac. Hist. Nat. B. Aires **32**:88. 1923, not Wallr.—Lower side of leaves glabrescent.

f. FARINOSUM (S. Wats.) Aellen, l.c. 43.—*Ch. murale* var. *farinosum* S. Wats. in Proc. Am. Acad. **9**:97. 1874.—*Blitum rubrum* var. *hypoleuca* Speg. in Anal. Mus. Nac. B. Aires, 2e sér., **4**:141. 1902.—*Ch. rubrum* var. *hypoleuca* Hauman et Irigoyen in Anal. Mus. Nac. Hist. Nat. B. Aires **32**:88. 1923.—Lower side of leaves copiously farinose.

f. LATIFOLIUM Thellung et Aellen l.c. :43.—Leaves as broad as long, with hastate base.

f. ANGUSTIUS Thellung et Aellen l.c. :44.—Here belongs f. *nanum* Aellen, l.c. 44.—Plant small, branches 2-3 cm. long; leaves small, less than 1 cm. long, entire.

Bolivia, Lake Titicaca.

Sect. VI. EUBLITUM (Moq.) Aellen in Verh. Naturf. Ges. Basel **41**:103. 1930.—*Eublitum* Moq. Chenop. enum. 47. 1840, as a section of *Blitum*.

Perianth when attached to fruit mostly fleshy, red, with 3 (-5) attenuated tips. Seeds vertical or horizontal in terminal flowers. Leaves becoming glabrous. Stigma short.

KEY TO SECTION EUBLITUM

1. Leaves hastate, entire ..... 13. *Ch. Overi*
1. Leaves hastate, dentate.
   2. Inflorescence bracteate ..... 14. *Ch. foliosum*
   2. Inflorescence almost ebracteate ..... 15. *Ch. capitatum*

13. CHENOPODIUM OVERI Aellen in Fedde Rep. spec. nov. **26**:159. 1929. —*Blitum hastatum* Rydb. in Bull. Torr. Bot. Club **28**:273. 1901.

Wyoming to Oregon, Nevada and New Mexico.

14. CHENOPODIUM FOLIOSUM (Moensch) Aschers. Fl. Brand. **1**:572. 1864.—*Morocarpus foliosus* Moench Meth. 342. 1794.—*Blitum virgatum* L. Spec. Pl. 4. 1753.—*Ch. virgatum* Jessen Deutsche Exc.-Fl. 300. 1879, not Thbg. 1815.

Adventive in Massachusetts, New York, Idaho, Oregon and Washington.

15. CHENOPODIUM CAPITATUM (L.) Asch. Fl. Brand. **1**:572. 1864.—*Blitum capitatum* L. Spec. Pl. 4. 1753.

Presumably adventive or naturalized in southern Canada and extending to New Jersey, Minnesota, New Mexico, and Oregon.

Sect. VII. PSEUDOBLITUM Hook. f. in Benth. et Hook. Gen. Pl. **3**:15. 1880 em. Aellen in Verh. Naturf. Ges. Basel **41**:102. 1930.

Like section *Degenia*, but perianth of lateral flowers 4-5-tipped and free almost to base. Seeds horizontal or vertical (in this case perianth separated).

KEY TO SECTION PSEUDOBLITUM

1. Leaves large, up to 5 cm. long (including the petiole-like base), up to 3.5 cm. wide, usually deltoid-hastate, sinuately dentate. Inflorescence a terminal panicle, bracteate only in lower part. Seed usually horizontal ..... 16. *C. mexicanum*
1. Leaves usually smaller, narrower, not hastate. Inflorescences usually axillary, rarely terminal, spicate or paniculate or cymose, mostly bracteate.
   2. Lower side of leaves farinose ..... 17. *Ch. glaucum*
      3. Leaves with short, petiole-like base, elongate, ovate-rhombic, distantly undulate-dentate ..... ssp. *eu-glaucum*
      3. Leaves with long, petiole-like base.
         4. Leaves broadly deltoid to rhombic, irregularly sinuately lobed to dentate, more or less trilobed, with few sharp teeth. Inflorescences few, small, with few flowers ..... ssp. *ambiguum*

4. Leaves rhombic to trilobed, irregularly sharply sinuate-dentate, usually smaller (than in ssp. *ambiguum*).
   5. Leaves as long as broad, slightly trilobed. Petiole longer than leaf.... ssp. *Parodii*
   5. Leaves longer than broad, hardly trilobed, sharply sinuate-dentate. Petiole as long or shorter than the leaf ..... ssp. *salinum*
2. Leaves on both sides glabrous or glabrescent, ovate-rhombic, irregularly sinuate-dentate to lobed, rarely entire. Glomerules in axillary or terminal spikes or panicles, rarely in ebracteate cymes ..... 18. *Ch. rubrum*

16. CHENOPODIUM MEXICANUM Moq. in DC. Prodr. **13**(2):70. 1849. Mexico.

17. CHENOPODIUM GLAUCUM L. Spec. Pl. 220. 1753.

ssp. EU-GLAUCUM Aellen in Fedde Rep. spec. nov. **26**:45. 1929.

Probably adventive from Europe. Canada: Alberta, Quebec. United States: Wyoming, Colorado, New Mexico, N. and S. Dakota, Nebraska, Iowa, Missouri, Illinois, Indiana, Michigan, Ohio, Vermont, Massachusetts, New York, Pennsylvania, New Jersey, Maryland, D. of Columbia, and Virginia.

ssp. AMBIGUUM (R. Br.) Thellung et Aellen in Fedde Rep. spec. nov. **26**:47. 1929.—*Ch. ambiguum* R. Br. Prodr. N. Holl. **1**:407. 1810.—*Ch. glaucum* var. *paschale* Fuentes in Inst. Centr. Meteor. y Geofis. Chile no. 4. 1913.

Chile: Easter Island, Chonos Archipelago.

ssp. **Parodii** Aellen comb. nov.—*Ch. Parodii* Aellen in Fedde Rep. spec. nov. **26**:49. 1929.

Argentina.

ssp. SALINUM (Standley) Aellen in Fedde Rep. spec. nov. **26**:46.1929.—*Ch. salinum* Standley in N. Am. Fl. **21**:29. 1916; Rydberg Fl. Rocky Mts. 242. 1917.

Alaska, represented by var. *pulchrum* Aellen in Fedde Rep. spec. nov. **26**: 47. 1929; plant reddish, upper leaves entire, oval-elliptic to broad lanceolate; Montana, Oregon, Idaho, Wyoming, Nevada, Colorado, Arizona, New Mexico, N. and S. Dakota, Missouri.

18. CHENOPODIUM RUBRUM L. Spec. Pl. 218. 1753.

f. HUMILE (Hook.) Asch. et Graeb. Syn. **5**(1):99. 1913.—*Ch. humile* Hook. Fl. Bor. Am. **2**:127. 1838.—Plant low, only a few cm. high; leaves entire, ovate-spatulate.

North America; the South American records are based on *Ch. macrospermum* Hook. f. ssp. *halophilum* (Phil.) Aellen.

Canada: Nova Scotia, Saskatchewan. United States: Washington, Montana, Oregon, Idaho, Wyoming, Utah, Colorado, New Mexico, North Dakota, Maine, New York.

Sect. VIII. THELLUNGIA Aellen in Verh. Naturf. Ges. Basel 41:103. 1930.

Perianth of lateral flowers (2-) 3-4-tipped, tips $^1/_2$-$^1/_3$ free, linear-cochleariform, seed vertical; perianth of terminal flowers 4-5-tipped, seed horizontal. Basal rosette of leaves; leaves 1-2-pinnate or pinnately lobed; flowers in bracteate glomerules on unbranched stems. One species.

19. CHENOPODIUM ANTARCTICUM (Hook. f.) Benth. et Hook. f.—*Blitum antarcticum* Hook. f. Fl. Antarc. 2:549. 1847.

Southern South America.

Sect. IX. AGATHOPHYTON (Moq.) Hook. f. in Benth. et Hook. Gen. Pl. 3:52. 1880; Moquin in DC. Prodr. 13(2):84. 1849, as a section of *Blitum*.—*Agathophytum* Moq. in Ann. sci. nat., 2e sér., 1:191. 1834, as genus.

Plants perennial. Perianth 4-5-tipped, tips fused to about the middle, broad, ligulate, irregularly sinuate-dentate. Stigmas 2 (-3), long. Seeds vertical.

KEY TO SECTION AGATHOPHYTON

1. Leaves entire, rarely sinuate-dentate ..... 20. *Ch. Bonus Henricus*
1. Leaves deeply and sharply sinuate-dentate ..... 21. *Ch. californicum*

20. CHENOPODIUM BONUS HENRICUS L. Spec. Pl. 218. 1753.

Introduced from Europe; Nova Scotia and Quebec to Delaware and Iowa.

21. CHENOPODIUM CALIFORNICUM S. Wats. in Bot. Calif. 2:48. 1880. —*Blitum californicum* S. Wats. in Proc. Am. Acad. 9:101. 1874.—*Blitum Bonus Henricus* var. *erosum* Moq. in DC. Prodr. 13(2):85. 1849.

Sect. X. CHENOPODIA (C. A. Mey.) em. Aellen in Fl. URSS. 6:54. 1936. —Sect. *Chenopodia* C. A. Meyer in Ledeb. Fl. Alt. 1:403. 1829, in part.—Sect. *Chenopodiastrum* Moq. in DC. Prodr. 13(2):61. 1849, in part.

Perianth with five tips, herbaceous, mostly somewhat keeled. Leaves variable, lanceolate to rhomboidal or cordate to oval. Plants glabrous or with vesiculose hairs. Seeds horizontal. Subsections based on structural differences of seed surfaces.

Subsect. 1. LEJOSPERMA Aellen et Iljin in Fl. URSS. 6:59. 1936.

Seeds smooth or nearly smooth, with indistinct ridges or irregularly and slightly pitted.

KEY TO SUBSECTION LEJOSPERMA

1. Leaves linear, narrowly lanceolate or elongate, entire, slightly trilobed or hastate.
  2. Leaves linear, entire, 1-nerved.
    3. Seeds larger than 1 mm. in diam.
      4. Seed 1.5 mm. in diam. Pericarp free, ivory-white. Plant glabrous, bright green. Branches erect or divaricate ..... 22. *Ch. subglabrum*
      4. Seed 1-1.5 mm. in diam. Pericarp attached, red, glabrous or slightly farinose. Perianth tips divaricate at maturity ..... 23. *Ch. cycloides*
    3. Seed less than 1 mm. (0.8 mm.) in diam. Pericarp attached, ivory-white.

Plant densely farinose. Perianth tips closely enveloping the utricle ..... 24. *Ch. leptophyllum*

2. Leaves narrowly lanceolate or oblong, entire or slightly trilobed or hastate, three-nerved (the upper ones 1-nerved).
3. Pericarp adherent. Plant with a rank odor. Leaves entire ..... 25. *Ch. hians*
3. Pericarp not adherent. Plant without a rank odor.
4. Leaves hastate, with small lateral lobes at the leaf base, median lobe long, almost linear ..... 26. *Ch. papulosum*
4. Leaves narrowly lanceolate and entire or oblong and slightly trilobed, lobes somewhat below the middle of the leaf ..... 27. *Ch. pratericola*
5. Plant erect, tall. Leaves linear or narrowly lanceolate, the lower ones often somewhat trilobed ..... ssp. *eu-pratericola*
6. Leaves narrowly lanceolate or linear, usually entire ..... var. *Thellungianum*
6. Leaves broadly lanceolate, the lower and middle ones somewhat trilobed ..... var. *leptophylloides*
5. Plant low, usually diffusely branched. Leaves oblong, entire ..... ssp. *desiccatum*

1. Leaves rhombic or triangular or broadly lanceolate.
2. Young leaves and inflorescence bright-red. Leaves large, 5-20 cm. long and broad, profusely lobed-dentate. Plant 1-3 m. tall, robust ..... 28. *Ch. giganteum*
2. Plants green, rarely reddish. Leaves 1-10 cm. long, lobed-dentate or entire.
3. Plant usually small, delicate, profusely branched from base. Leaves small, rhombic-trilobed, median lobe often elongate. Without odor (South America) ..... 29. *Ch. carnosulum*
3. Plants usually robust, 20-200 cm. tall, without rank odor (prostrate, with rank odor—*Ch. Vulvaria*). Leaves highly variable.
4. Plant glabrous or glabrescent.
5. Plant growing in woods, large but delicate. Leaves oblong-ovoid to lanceolate, the upper ones entire, the lower ones with few teeth, thin ..... 30. *Ch. Standleyanum*
5. Plant growing as a robust weed. Leaves triangular to rhombic, often sharply dentate, fleshy ..... 31. *Ch. urbicum*
4. Plant farinose or, if glabrescent, dark-green.
5. Perianth tips free almost to the base, narrow at the base. Leaves trilobed, densely farinose on the lower side ..... 32. *Ch. cordobense*
5. Perianth tips fused to the middle, more or less triangular.
6. Leaves broadly triangular-rhombic, at base almost obtuse, with a simple or double lobate tooth (*Ch. petiolare* highly variable). Inflorescence paniculate, terminal.
7. Pericarp not adherent.
8. Seed with crispulate surface markings ..... 33. *Ch. Fremonti*
8. Seed with slightly rugulose surface markings ..... 34. *Ch. pilcomayense*
7. Pericarp adherent. Seed surface with delicate radial ridges..... 35. *Ch. petiolare*
6. Leaves rhombic, entire or dentate or trilobed, not obtuse at base.
7. Plant with a rank odor, prostrate or ascending. Leaves rhombic-ovate to roundish ..... 36. *Ch. Vulvaria*
7. Plants without a rank odor.
8. Leaves usually triangular, as long or a little longer than wide.

9. Median lobes broadly obtuse. Petioles of large leaves often longer than the lamina. Plant loosely branched, the branches long, mostly farinose. Inflorescence cymose..... 37. *Ch. opulifolium*

9. Median lobes acute. Petioles as long or shorter than the blades. Plants low, diffusely branched.

10. Plants densely farinose .....38. *Ch. incanum*

10. Plants farinose to glabrescent.

11. Plant delicate, with delicate branches, perianth tips not subulate and at most slightly carinate. Seed smooth, slightly pitted with some undulate lines (see above) .....29. *Ch. carnosulum*

11. Plant more robust, with strong branches, perianth tips subulate and carinate. Seed larger, not smooth, irregularly punctate ..... 39. *Ch. pallidicaule*

8. Leaves highly variable, linear to rhombic, often indistinctly trilobed (the lower teeth larger than the upper ones), entire or dentate.

9. Leaves ovate-rhombic, entire or the larger ones with a blunt tooth .....40. *Ch. atrovirens*

9. Leaves either more acute or more sharply dentate.

10. Leaves round or rhombic, profusely sinuate-dentate, with long cuneate base, median lobe short and with almost parallel margins, lowest tooth normally situated above the middle .....41. *Ch. Zobelii*

10. Leaves not round or rhombic, not profusely sinuate-dentate.

11. Plants or at least leaves farinose.

12. Whole plant farinose. Leaves oblong-rhombic, dentate. Median lobe acute. Inflorescence glomerulose-paniculate ..... 44. *Ch. albescens*

12. Leaves farinose, mostly ovate-rhombic to lanceolate. Inflorescence glomerulose-spicate or paniculate or cymose ..... 46. *Ch. album*

11. Plants pubescent when young, otherwise glabrescent (except *Ch. missouriense* var.)

12. Perianth strongly keeled.

13. Seed 1.25 mm. in diam. Inflorescence paniculate-glomerate, the glomerules small, delicate, usually 1.5-2.5 mm. in diam. Leaves oblong-rhombic, slightly trilobed with acute and dentate median lobe ..... 43. *Ch. missouriense*

13. Seed 1 mm. in diam. Inflorescence spicate. Leaves broadly rhombic, in the lower part lobed-dentate, median lobe acuminate (appearance of *Ch. album* x *Ch. Berlandieri* ssp. *Zschakei*) ..... 45. *Ch. Covillei*

12. Perianth slightly keeled. Leaves ovate-elliptic, typically with almost parallel margins and short cuneate base, upper ones lanceolate ..... 42. *Ch. strictum*

22. CHENOPODIUM SUBGLABRUM (S. Wats.) Nelson in Bot. Gaz. **34**:362. 1902.— *Ch. leptophyllum* var. *subglabrum* S. Wats. in Proc. Amer. Acad. 9:95. 1874.

Washington, Montana, South Dakota, Nebraska.

23. CHENOPODIUM CYCLOIDES A. Nelson in Bot. Gaz. **34**:363. 1902.
New Mexico, Kansas.

24. CHENOPODIUM LEPTOPHYLLUM Nutt. apud Moquin in DC Prodr. **13**(2):71. 1879, not of authors.—*Ch. album* var. *leptophyllum* Moq. l.c., in part.—*Ch. inamoenum* Standley in N. Am. Fl. **21**:15. 1916.

Montana, Oregon, Wyoming, Nevada, Utah, Colorado, Arizona, New Mexico, Texas.

25. CHENOPODIUM HIANS Standley in N. Am. Fl. **21**:16. 1916.

Wyoming, Nevada, Utah, New Mexico.

26. CHENOPODIUM PAPULOSUM Moq. in DC. Prodr. **13**(2):61. 1849.—*Ch. rafaelense* Chodat et Wilczek in Bull. Herb. Boiss., 2e sér., **2**:534. 1902.
Argentina.

27. CHENOPODIUM PRATERICOLA Rydb. in Bull. Torr. Bot. Club **39**:310. 1912.—*Ch. leptophyllum* of authors, not of Nutt.

ssp. **eu-pratericola** Aellen, ssp. nov.—Planta erecta. Folia linearia aut anguste-lanceolata, inferioribus saepe ± trilobatis.

Washington, Idaho, Montana, Oregon, Nevada, Utah, Wyoming, Colorado, California, Arizona, New Mexico, North and South Dakota, Nebraska, Iowa, Kansas, Missouri, Illinois, Indiana, New Jersey, Oklahoma, Texas, Louisiana, Virginia. Mexico, Argentina.

var. THELLUNGIANUM Aellen in Ostenia: 100. 1933.—*Ch. pratericola* Rydb. and *Ch. leptophyllum* of authors, s. str.

f. RUBRICAULE Blom apud Aellen in Fedde Rep. spec. nov. **26**: 134. 1929.

var. **leptophylloides** (Murr) Aellen, comb. nov.—*Ch. pratericola* var. *leptophylloides* Aellen in Ostenia :100. 1933.—*Ch. leptophyllum* var. *leptophylloides* Thellung et Aellen in Fedde Rep. spec. nov. **26**:134. 1929. *Ch. petiolare* var. *leptophylloides* Murr in Bull. Herb. Boiss., 2e sér., **4**:994. 1904.—*Ch. leptophyllum* var. *oblongifolium* of authors, not of S. Wats.

ssp. DESICCATUM (A. Nelson) Aellen in Fedde Repert. spec. nov. **26**: 136. 1929.—*Ch. desiccatum* A. Nelson in Bot. Gaz. **34**: 362. 1902.—*Ch. leptophyllum* var. *oblongifolium* S. Wats. in Proc. Am. Acad. 9:95. 1874, not of authors.—*Ch. oblongifolium* Rydb. in Bull. Torr. Bot. Club **33**:137. 1906.

Montana, Idaho, Wyoming, California, Arizona, New Mexico, South Dakota, Nebraska.

28. CHENOPODIUM GIGANTEUM Don Prodr. Pl. Nepal. 75. 1825.—*Ch. amaranticolor* Coste et Reynier in Bull. Soc. Bot. France **54**:178. 1907.

Southern Georgia (?), northern Florida (?), Cuba (?); Argentina.

29. CHENOPODIUM CARNOSULUM Moq. in DC. Prodr. **13**(2):64. 1849. —*Ch. patagonicum* Phil. in Anal. Univ. Santiago **91**:421. 1895.—*Ch. fuegianum* Speg. in Anal. Mus. Nac. B. Aires **5**:72. 1896-97.—*Ch. scabricaule* Speg. in Anal. Mus. Nac. B. Aires, 2e sér. 4, **7**:138. 1902.

Spegazzini (l.c.) described three forms under *Ch. scabricaule:*

f. **pusilla** (Speg.) Aellen, comb. nov.—Plant small, 2-5 cm. high. Leaves rhombic-trilobed. Seed 1 mm. in diam.

f. **robusta** (Speg.) Aellen, comb. nov.—Plant 15-20 cm. high. Leaves hastate-trilobed. Seed 1.25-1.5 mm.

f. **megalospermum** (Speg.) Aellen, comb. nov.—Plant 10-15 cm. high. Leaves also hastate-trilobed. Seed 1.5-2 mm.

Mexico; Ecuador, Bolivia, Chile, Argentina.

30. CHENOPODIUM STANDLEYANUM Aellen in Fedde Rep. spec. nov. **26**: 153. 1929.—*Ch. Boscianum* Moq. Chenop. enum. 21. 1840—and of authors, in part.—*Ch. album* var. *Boscianum* A. Gray Man. ed. 5. 407. 1867.—*Ch. polyspermum* var. *spicatum* A. Gray Man. ed. 2. 363. 1856. (cf. *Ch. Berlandieri* ssp. *Boscianum* [Moq.] Aellen).

South Dakota, Minnesota, Nebraska, Iowa, Kansas, Missouri, New Mexico, Texas, Illinois, Indiana, Ohio, Pennsylvania, Virginia, West Virginia, Florida.

31. CHENOPODIUM URBICUM L. Spec. Pl. 218. 1753.

Adventive in Minnesota, Missouri, Illinois. (Standley in N. Am. Fl. **21**: 12. 1916: "sparsely adventive from Nova Scotia to Ontario, Missouri, and Maryland").

Chile.

32. CHENOPODIUM CORDOBENSE Aellen in Fedde Rep. spec. nov. **26**:152. 1929.

Argentina.

33. CHENOPODIUM FREMONTI S. Wats. Bot. King's Expl. 287. 1871.

Canada: British Columbia. United States: Montana, Oregon, Idaho, Wyoming, Nevada, Utah, Colorado, Arizona, New Mexico, North and South Dakota, Nebraska, Texas, Mexico.

f. FARINOSUM Aellen in Fedde Rep. spec. nov. **26**:142. 1929.—Whole plant more or less farinose.

var. PRINGLEI (Standley) Aellen in Fedde Rep. spec. nov. **26**:142. 1929.—*Ch. Pringlei* Standley in N. Am. Fl. **21**:18. 1916.—Leaves deeply sinuate-dentate.

South Dakota. Mexico.

Fosberg (1941) recognizes three varieties of this species, namely var. *fremontii* Fosberg, *incanum* Wats., and *atrovirens* (Rydb.) Fosberg, and reinstates *Ch. nevadense* Standley (see no. 38a of this synopsis). As Fosberg suggests, the whole complex should be studied carefully on the basis of local distribution and possible hybridization.

34. CHENOPODIUM PILCOMAYENSE Aellen in Fedde Rep. spec. nov. **26**: 152. 1929.

Argentina.

35. CHENOPODIUM PETIOLARE H.B.K. in Humb. et Bonpl. Nov. Gen. et Sp. Pl. **2**:191. 1817.—*Ch. paniculatum* Hook. Bot. misc. **2**:237. 1831.—*Ch. sparsiflorum* Phil. in Anal. Univ. Santiago **91**:419. 1895.—*Ch. bolivianum* Murr in Mag. Bot. Lap. **1**:359. 1902, in part.—*Ch. Fremonti* Murr in Allg. Bot. Zeitschr. **12**:54-55. 1906. and in Bull. Herb. Boiss., 2e sér., **4**:994. 1904, not of S. Wats.

Ecuador; Peru; Bolivia; Chile; Argentina.

Can be divided as follows:

f. INCANUM (Murr) Aellen in Fedde Rep. spec. nov. **26**:150. 1929.—*Ch. paniculatum* var. *incanum* Murr in Allg. Bot. Zeitschr. **12**:54-55. 1906.—Plant more or less farinose.

f. HOOKERI Aellen, l.c.—Leaves almost glabrous.

f. HASTATUM Aellen, l.c.—Leaves with divergent tips of hastate lobes.

f. SCUTATUM Aellen, l.c. :151.—Leaves with hastate tips pointing slightly downward.

f. TRILOBUM Aellen, l.c. :151.—Leaves clearly trilobed, the broader lateral lobes bilobed.

f. RENIFORME (Murr) Aellen, l.c. :151.—*Ch. paniculatum* var. *reniforme* Murr in Bull. Herb. Boiss., 2e sér., **4**:994. 1904.—Leaves partly reniform to cordate.

36. CHENOPODIUM VULVARIA L. Spec. Pl. 220. 1753.

California. According to Standley in N. Am. Fl. **21**:20. 1916: "Sparsely adventive from Quebec and Ontario to Maryland and Wisconsin, and in Florida."

37. CHENOPODIUM OPULIFOLIUM Schrader in Koch et Ziz, Cat. pl. Palat. 6. 1814.—*Ch. viride* Standley in N. Am. Fl. **21**:21. 1916, in part.—? *Ch. flabellifolium* Standley, l.c. 19.

Adventive in Maryland and Illinois.

38. CHENOPODIUM INCANUM (S. Wats.) A. Heller in Pl. World **1**:23. 1897.—*Ch. Fremonti* var. *incanum* S. Wats. in Proc. Am. Acad. **9**:94. 1874.

See comment under 33. *Ch. Fremonti* S. Wats. and under 38a. *Ch. nevadense* Standley.

California, Nevada, Utah, Colorado, Arizona, New Mexico, South Dakota, Nebraska, Kansas, Missouri, Oklahoma, Texas. Mexico.

Ch. deltaphyllum Osterhout in Bull. Torr. Bot. Club **57(8)**:559. 1931 may belong here or to the *Fremonti* complex as defined by Fosberg, either in synonymy or as a variety or form.

38a. CHENOPODIUM NEVADENSE Standley in N. Am. Fl. **21**:16, 1916.—Aellen considered this species identical with *Ch. incanum* (Wats.) Heller, as is evident from his annotations on the type sheet (*fide* Fosberg 1941, p. 691). Fosberg (l.c.) reinstated the species and pointed out several distinctive characters. These are: leaves much smaller, less numerous, and less conspicuous than in *Ch. incanum* (Wats.) Heller; flowers in small glomerules or single and prominently pedicellate, mixed, in large, very diffuse panicles making up the upper half to three-fourths of the plant; branching is conspicuously cymose, individual branches becoming even scorpioid; the most notable character is the presence of numerous solitary pedicellate flowers; seed very small, 0.7-0.9 mm. in diam., quite thick; pericarp adherent. See Fosberg 1941, pp. 692-693, for illustrations.

Nevada.

39. CHENOPODIUM PALLIDICAULE Aellen in Fedde Rep. spec. nov. **26**:126. 1929.—*Ch. canihua* Cook in Jour. Heredity **16**:37. 1925 (with photo, but without description).

Peru, Bolivia.

f. PURPUREUM Aellen, l.c.—Whole plant bright red.

40. CHENOPODIUM ATROVIRENS Rydberg in Mem. N. Y. Bot. Gard. **1**:131. 1900.—*Ch. Wolfii* Rydb. in Bull. Torr. Bot. Club **30**:248. 1903.—*Ch. aridum* A. Nelson in Bull. Torr. Bot. Club **31**: 240. 1904.

Montana, Wyoming, California, Nevada, Utah, Colorado, New Mexico, North Dakota.

41. CHENOPODIUM ZOBELII Ludwig et Aellen in Fedde Rep. spec. nov. **26**:131. 1929.

Argentina.

42. CHENOPODIUM STRICTUM Roth in Nov. pl. spec. Ind. or. 180. 1821; Aellen in Mag. Bot. Lap. Bot. **27**:105. 1928. Can be divided in:

ssp. STRIATUM (Krasan) Aellen et Iljin in Fl. URSS. **6**:65. 1936.—*Ch. album* var. *striatum* Kras. in Mitth. Naturw. Verein Steierm. **30**:254. 1893.—Leaves elongate, deeply serrate, often with red margins. Inflorescence glomerulose, spicate.

Native of Orient and southern Asia. Not definitely known to occur in America.

ssp. **glaucophyllum** Aellen, comb. nov.—*Ch. glaucophyllum* Aellen in

Fedde Rep. spec. nov. **26**:155. 1929.—Leaves ovate-lanceolate, mostly entire. Inflorescence glomerulose, cymose.

South Dakota, Minnesota, Missouri.

43. CHENOPODIUM MISSOURIENSE Aellen in Bot. Not. Lund: 206. 1928; Aellen in Fedde Rep. spec. nov. **26**:155. 1929.—*Ch. paganum* Standley in N. Am. Fl. **21**:23. 1916, in part, not Rchb.

Missouri, Tennessee.

var. BUSHIANUM Aellen in Fedde Rep. spec. nov. **26**:156. 1929.—Leaves definitely farinose on lower side.

Missouri, Indiana.

44. CHENOPODIUM ALBESCENS Small Fl. SE. U.S. 385, 1903.—*Ch. Berlandieri* ssp. *Zschakei* var. *glaucoviride* Aellen in Fedde Rep. spec. nov. **26**:58. 1929.

Texas, Arizona, Iowa.

45. CHENOPODIUM COVILLEI Aellen in Fedde Rep. spec. nov. **26**:153. 1929. (Appearance of *Ch. album* x *Berlandieri* ssp. *Zschackei*).

Oregon.

46. CHENOPODIUM ALBUM L. Spec. Pl. 219. 1753.

ssp. EU-ALBUM (Ludwig) Aellen.—*Ch. album* ssp. *eu-album* Ludwig in Asch. and Graeb. Syn. **5**:40. 1913, in part.—Leaves ovate-rhombic to rhombic or ovate-lanceolate to lanceolate, mostly irregularly sinuate-dentate, often slightly trilobed. Inflorescence spicate, paniculate or cymose.

var. **polymorphum** Aellen, var. nov.—*Ch. album* var. *eu-album* Ludwig in Schinz und Keller Fl. Schweiz **2**:95. 1914, in part.—Folia paulum trilobata (deinde rhombica), lobus medius paulatim apicem versus attenuatus aut folia integerrima (tum plerumque oblongo-ovalia ad lanceolata) aut irregulariter dentata.

Leaves slightly trilobed (and then ± rhombic), median lobes attenuated towards the tips, or leaves entire (and then mostly lanceolate-ovate to lanceolate) or irregularly dentate.

Throughout North America. Adventive? Sporadic in Ecuador, Chile, Brazil, and Argentina.

f. **spicatum** (Koch) Aellen, comb. nov.—*Ch. album* var. *spicatum* Koch Syn. Fl. Germ. 606. 1837.—Leaves dentate, farinose. Inflorescence densely spicate, erect.—Depauperate growth form of dry localities.

f. **glomerulosum** (Rchb.) Aellen, comb. nov.—*Ch. glomerulosum* Fl. Germ. exc. 579. 1832.—Leaves mostly ovate-rhombic, slightly farinose. Inflorescence loosely glomerulose, paniculate.—Most common form.

f. **cymigerum** (Koch) Aellen, comb. nov.—*Ch. album* var. *cymigerum* Koch Syn. Fl. Germ. 606. 1837.—*Ch. viride* of most authors, not of

Linnaeus.—Leaves ovate-lanceolate, mostly entire to dentate (few teeth), slightly farinose to glabrous. Inflorescence cymose.

f. **lanceolatum** (Muhl.) Aellen, comb. nov.—*Ch. lanceolatum* Muhl. in Willd. Enum. 291. 1809.—Plant often large. Leaves small, acuminate, dentate, lower side becoming glabrous. Inflorescence glomerulose, paniculate.

var. **Borbasii** (Murr) Aellen, comb. nov.—*Ch. Borbasii* Murr in Progr. Oberr. Innsbr. 56. 1891.—Lower third of leaves mostly with a large lobe, the median lobe with nearly parallel margins, rather blunt. Inflorescence pyramidal, paniculate.

Not definitely recorded from America.

var. **microphyllum** (Boenn.) Aellen, comb. nov.—*Ch. microphyllum* Boenn. Fl. Monast. 1824.—Leaves small, at most 3 cm. long; ovate-lanceolate, nearly entire or irregularly sinuate-dentate. Inflorescence paniculate. Glomerules small, olive green.

District of Columbia.

var. **Stevensii** Aellen, comb. nov.—*Ch. album* var. *Stevensii* Aellen in Fedde Rep. spec. nov. **26**:130. 1926.—Leaves oblong-ovate, slightly below the middle with 1-2 large teeth, otherwise entire or slightly dentate, with long, cuneate base (the lower veins originate 0.5 cm. above the leaf base). Inflorescence bracteate, short, axillary, densely glomerulose.

North Dakota.

var. **dacoticum** Aellen, comb. nov.—*Ch. album* var. *dacoticum* Aellen in Fedde Rep. spec. nov. **26**:131. 1929.—Leaves large, to 8 cm. long, triangular-rhombic, deeply lobed, doubly dentate. Petiole short, ¾ of lamina. Inflorescence small, spicate.

North Dakota.

ssp. FALLAX Aellen in Bot. Not. Lund: 208. 1928.—Lower and median leaves broadly ovate-rhombic, with short and broad leaf basis, lower teeth placed low, profusely sinuate-dentate, tip usually obtuse or almost truncate. Petiole $^1/_3$-$^1/_2$ of lamina. Inflorescence short, spicate, bracteate.

North Dakota.

Subsect. 2. CELLULATA Aellen et Iljin in Fl. URSS. **6**:59. 1936.—Seed surfaces indistinctly marked or distinctly alveolate.

KEY TO SUBSECTION CELLULATA

1. Alveolae of seed surface abutting.
   2. Plant with a rank odor, copiously farinose. Leaves broadly rhombic-ovate, the lower part with a lateral divaricate tooth, otherwise entire or dentate..... 47. *Ch. Watsoni*
   2. Plant generally without rank odor (except some forms of *Ch. Berlandieri* ssp. *eu-Berlandieri* and ssp. *Zschackei*).
      3. Seed less than 1 mm. (0.8-0.9 mm.) in diam. Leaves linear, median lobe linear, long, with almost parallel margins ..... 48. *Ch. serotinum*

3. Seeds larger than 1 mm. in diam.
   4. Seed 1-1.5 mm. in diam., black. Leaves ovate or elliptic or rhombic, quite wide. Median lobe obtuse or acuminate ..... 49. *Ch. Berlandieri*
      5. Greatest width of leaves at or above the middle or, if lateral lobes below the middle are present, then leaves more or less ovate with a rather obtuse median lobe.
         6. Leaves small, 1-3 cm. long, 0.5 cm. wide, ovate-lanceolate, the upper ones lanceolate to linear and entire, the lower ones with two small lateral teeth and several minor ones ..... ssp. *Boscianum*
         6. Leaves large, ovate or elliptic or ovate-rhombic, somewhat trilobed; lateral lobes usually at or above the middle ..... ssp. *Zschackei*
            7. Plant copiously farinose, ivory-white.
               8. Leaves short, obtuse, slightly trilobed, often with a rank odor ..... var. *foetens*
               8. Leaves larger, ovate-elliptic, dentate, without odor ..... var. *farinosum*
            7. Plant farinose or glabrescent.
               8. Lateral lobes below the middle of leaf, distal part of leaf obtuse ..... var. *californicum*
               8. Lateral lobes usually at or above the middle of the leaf ..... var. *typicum*
      5. Greatest width of leaf below the middle of the blade.
         6. Leaves oblong-lanceolate, almost entire ..... ssp. *Esauae*
         6. Leaves sharply dentate.
            7. Leaves indistinctly trilobed, but even the upper ones sharply and profusely dentate ..... ssp. *yucatanum*
            7. Leaves distinctly trilobed.
               8. Lateral lobes well developed, often divaricate and bipartite. Median lobe at least near base with almost parallel margins.
                  9. Inflorescence terminal, ebracteate, paniculate-pyramidal with divaricate branches. Plant foetid ..... ssp. *eu-Berlandieri*
                  9. Inflorescence glomerulose-spicate, bracteate. Plant not foetid ..... ssp. *pseudo-petiolare*
               8. Lateral lobes not divaricate, median lobe acuminate.
                  9. Leaves at the base broadly rounded to acuminate. Lateral lobes tooth-like. Median lobe wide, with few to many teeth ..... ssp. *platyphyllum*
                  9. Leaves cuneate at the base, smaller. Median lobe narrowly triangular, acute, entire or slightly dentate ..... ssp. *Ludwigianum*
   4. Leaves broadly trilobed, with a broadly triangular median lobe. Seed large, 1.5-1.75 mm. in diam., black ..... 50. *Ch. Quinoa* ssp. *Milleanum*

1. Canals separating the alveolae of the seed surface (here belong also *Ch. album* x *Berlandieri* and a few plants of *Ch. Quinoa* ssp. *Milleanum*).
   2. Seed with acute margin ..... 51. *Ch. lenticulare*
   2. Seeds with rounded margin.
      3. Plants foetid.
         4. Plant delicate. Leaves triangular, slightly lobed-dentate, with acute median lobes ..... 52. *Ch. arizonicum*
         4. Plant robust. Most leaves definitely trilobed, with wide lateral lobes

and a nearly linear median lobe ..... 53. *C. hircinum*

5. Larger leaves more or less trilobed or with well developed lower lateral teeth.

6. Seed with a maximum diam. of 1.1 mm. ..... ssp. *eu-hircinum* var. *typicum*

6. Seed 1.5-2 mm. in diam. ..... ssp. *catamarcense*

5. Larger leaves ovate-rhombic, slightly trilobed, profusely dentate ..... ssp. *eu-hircinum* var. *andinum*

3. Plants not foetid.

4. Leaves linear, entire. Plant glabrous ..... 54. *Ch. pallescens*

4. Leaves dentate or lobed. Plants farinose.

5. Alveolae indistinct, shallow. Leaves broadly trilobed, profusely and sharply dentate ..... 55. *Ch. viride*

5. Alveolae quite distinct, deep. Leaves not trilobed.

6. Seeds 1.25-2.5 mm. in diam. Perianth loosely adhering to the fruit. Plants large or, at least, robust.

7. Perianth dark green or almost black. Leaves broadly rhombic to broadly ovate-rhombic. Seed large, 2.-2.5 mm. in diam. (rarely 1.25-1.5 mm.) ..... 56. *Ch. Bushianum*

7. Perianth yellow, large, almost stellate when spread out..... 57. *Ch. macrocalycium*

6. Seed 1-1.25 mm. in diam. Perianth firmly enveloping the fruit. Plant small. Leaves ovate to lanceolate, with a simple tooth in the middle or entire ..... 58. *Ch. Philippianum*

47. CHENOPODIUM WATSONI A. Nelson in Bot. Gaz. **34**:362. 1902.
Colorado, Arizona, New Mexico, South Dakota.

f. GLABRESCENS Aellen in Fedde Rep. spec. nov. **26**:120. 1929. —*Ch. neomexicanum* Standley in N. Am. Fl. **21**:19. 1916.—Plant green slightly farinose or glabrous.
New Mexico.

48. CHENOPODIUM SEROTINUM L. Cent. pl. **2**:12, 1756, in part.—*Ch. ficifolium* Smith Fl. Brit. **1**:276. 1800.
Eurasia; may be found adventive in America.

49. CHENOPODIUM BERLANDIERI Moq. Chenop. enum. 23. 1840.—Polymorphic species.

ssp. BOSCIANUM (Moq.) Aellen in Fedde Rep. spec. nov. **26**:61. 1929. —*Ch. Boscianum* Moq. Chenop. enum. 21. 1840, in part.
Missouri, Louisiana, Virginia, North Carolina, Alabama, Florida.

ssp. ZSCHACKEI (Murr) Zobel Verz. Anhalt. Phanerog. **3**:70. 1909.—*Ch. Zschackei* Murr in Deutsche Bot. Monatsschr. **19**:39. 1901.—*Ch. album* for most part of American authors, not of Linnaeus.

var. FOETENS (Ludwig) Aellen in Fedde Rep. spec. nov. **26**:57. 1929.—*Ch. Berlandieri* Rasse *foetens* Ludwig in Asch. and Graeb. Syn. **5**:83. 1913.
South Dakota, Missouri, Texas.

f. INTEGRUM Aellen, l.c.—Plant small. Leaves entire or slightly dentate.

var. FARINOSUM (Ludwig) Aellen in Fedde Rep. spec. nov. **26**:56. 1929.—*Ch. Berlandieri* Rasse *farinosum* Ludwig in Asch. and Graeb. Syn. **5**: 82. 1913.—*Ch. dacoticum* Standley in N. Am. Fl. **21**:22. 1916.

Colorado, New Mexico, South Dakota, Missouri.

var. CALIFORNICUM Aellen in Fedde Rep. spec. nov. **26**:57. 1929. California.

var. TYPICUM (Ludwig) Aellen in Fedde Rep. spec. nov. **26**:52. 1929.—*Ch. Berlandieri* var. *typicum* Ludwig in Asch. and Graeb. Syn. **5**:81. 1913.

Oregon, Idaho, Montana, Wyoming, California, Nevada, Utah, Colorado, Arizona, New Mexico, North and South Dakota, Minnesota, Kansas, Missouri, Oklahoma, Texas, Louisiana, Illinois. Mexico.

Varies as follows:

f. ANGUSTIUS (Ludwig) Aellen in Fedde Rep. spec. nov. **26**: 55. 1929.—*Ch. Berlandieri* var. *typicum* f. *angustius* Ludwig in Asch. and Graeb. Syn. **5**:82. 1913.—Leaves narrower, with a longer tip.

f. LATIFOLIUM (Ludwig) Aellen, l.c.—*Ch. Berlandieri* var. *typicum* f. *latifolium* Ludwig, l.c.—Leaves broader, often somewhat round.

f. DENTATUM Aellen, l.c.—Leaves profusely dentate.

f. PEDUNCULARE Aellen, l.c. — Terminal inflorescence large, cymose.

f. NEGLECTUM Aellen, l.c.—Inflorescence short, axillary, cymose.

f. PURPURASCENS Ludwig et Aellen in Fedde Rep. spec. nov. **26**:56. 1929.—Mature plant colored red.

f. GRACILE Aellen, l.c. :56.—Plant small, 1-2 dm. high. Leaves a few centimeters long.

f. GROSSUM Aellen, l.c. :56.—Perianth 3 mm. wide. Glomerules 6-8 mm. in diam. Inflorescence cymose.

ssp. ESAUAE Aellen in Fedde Rep. spec. nov. **26**:59. 1929. California, Idaho (?), South Dakota (?).

ssp. YUCATANUM Aellen in Fedde Rep. spec. nov. **26**:59. 1929. New Mexico. Mexico.

ssp. EU-BERLANDIERI Aellen in Fedde Rep. spec. nov. **26**:62. 1929.—*Ch. Berlandieri* Moq. Chenop. enum. 23. 1840, s. str.—*Ch. Palmeri* Standley in N. Am. Fl. **21**:19. 1916.

Texas. Mexico.

ssp. PSEUDO-PETIOLARE Aellen in Fedde Rep. spec. nov. **26**:60. 1929.—*Ch. petiolare* of North American authors.

California, Nevada, Arizona, New Mexico, Kansas, Texas, Florida. Mexico.

ssp. PLATYPHYLLUM (Issler) Ludwig in Schinz u. Keller Fl. Schweiz 2:94. 1914.—*Ch. platyphyllum* Issler in Allg. Bot. Zeitschr. 8:193. 1901.
Washington, Oregon, Wyoming, Colorado.

var. OPULIFOLIFORME Aellen in Fedde Rep. spec. nov. 26:58. 1929. —Leaves triangular, with broadly spatulate base, trilobed with broad lateral lobes each with two teeth.
Nevada, New Mexico, South Dakota.

var. COLORADENSE Aellen, l.c. :59.—Leaves broadly triangular, obtuse at nearly right angles near base, not lobed, but profusely dentate.
Colorado.

ssp. LUDWIGIANUM Aellen in Fedde Rep. spec. nov. 26:59. 1929.—*Ch. ferulatum* Lunell in Am. Midl. Nat. 3: contents 4. 1914.
North Dakota.

50. **Chenopodium Quinoa** ssp. **Milleanum** Aellen comb. nov.—*Ch. hircinum* ssp. *Milleanum* Aellen in Fedde Rep. spec. nov. 26:122. 1929.
Ecuador.

51. CHENOPODIUM LENTICULARE Aellen in Fedde Rep. spec. nov. 26:152. 1929.
Texas.

52. CHENOPODIUM ARIZONICUM Standley in N. Am. Fl. 21:19. 1916.—*Ch. Parryi* Standley, l.c. :21.
Utah, Arizona. Mexico.

53. CHENOPODIUM HIRCINUM Schrader Ind. Sem. Hort. Gotting. :2. 1833.

ssp. EU-HIRCINUM Aellen in Fedde Rep. spec. nov. 26:120. 1929.
var. TYPICUM Ludwig et Aellen in Fedde Rep. spec. nov. 22:121. 1929. Polymorphic.

Colombia, Ecuador, Peru, Bolivia, Chile, Paraguay, Uruguay, Argentina. Elsewhere often adventive.

f. **genuinum** Aellen, f. nov.—Lobus medius ± parallelo-marginatus, paulum dentatus. Lobi laterales 1-2-dentati.

f. MULTIDENTATUM (Ludwig) Aellen in Fedde Rep. spec. nov. 26:121. 1929.—*Ch. hircinum* f. *multidentatum* Ludwig in Asch. and Graeb. Syn. 5:86.1913.—Median lobes profusely dentate.

f. **acutatum** (Ludwig) Aellen, comb. nov.—*Ch. hircinum* f. *acutatum* Ludwig, l.c.—Median lobes acute.

f. ANGUSTIFOLIUM (Ludwig) Aellen, l.c.—*Ch. hircinum* f. *angustifolium* Ludwig, l.c.—Leaves smaller; median lobes acute.

f. DEMINUTUM (Ludwig) Aellen, l.c. 122.—*Ch. hircinum* f.

deminutum Ludwig, l.c.—*Ch. hircinum* f. *microphyllum* Thellung ap. Parodi in Rev. Fac. Agr. Vet. 1(7):192. 1930.—Leaves smaller than in the typical plant.

f. **subtrilobum** (Issler) Aellen, comb. nov.—*Ch. trilobum* Issler in Allg. Bot. Zeitschr. 8:174. 1902.—*Ch. hircinum* var. *subtrilobum* Issler in Allg. Bot. Zeitschr. 10:43. 1904.—Leaves very small. Branches long and thin.

var. ANDINUM Aellen in Fedde Rep. spec. nov. 26:122. 1929.
Peru.

ssp. CATAMARCENSE Aellen in Fedde Rep. spec. nov. 26:122. 1929.
Argentina.

54. CHENOPODIUM PALLESCENS Standley in N. Am. Fl. 21:15. 1916.
New Mexico, Oklahoma.

55. CHENOPODIUM VIRIDE L. Spec. Pl. 219. 1753, not of most authors.
Northern Eurasia. Not definitely recorded from America.

56. CHENOPODIUM BUSHIANUM Aellen in Fedde Rep. spec. nov. 26:63. 1929.—*Ch. album* and *Ch. paganum* of most North American authors, in part; not of Linnaeus and Reichenbach.—*Ch. album* ssp. *Collinsii* Murr in Bull. Herb. Boiss., 2e sér., 4:990. 1904.

Canada. United States: from North Dakota to Arkansas, North Carolina and New York.

f. ACUTIDENTATUM Aellen, l.c. 119.—Leaves profusely and sharply dentate.

var. CINERASCENS Aellen, l.c. :119.—Perianth farinose, gray. Seed somewhat smaller.

57. CHENOPODIUM MACROCALYCIUM Aellen in Fedde Rep. spec. nov. 26:119. 1929.
Massachusetts.

58. CHENOPODIUM PHILIPPIANUM Aellen in Fedde Rep. spec. nov. 26: 123. 1929.
Chile.

Subsect. 3. UNDATA Aellen et Iljin in Fl. URSS. 6:54. 1936. Seed surface marked by distinct, undulate ridges.

KEY TO SUBSECTION UNDATA

1. Leaves ovate or ovate-rhombic, profusely dentate, irregularly sinuate-dentate to laciniate-serrate, more or less farinose, rather thick. Seed with acute margin ..... 59. *Ch. murale*

1. Leaves ovate to ovate-lanceolate, usually entire, thin. Seed with round margin..... 60. *Ch. polyspermum*

59. CHENOPODIUM MURALE L. Spec. Pl. 219. 1753.

Probably naturalized throughout the temperate and tropical regions of the Americas.

60. CHENOPODIUM POLYSPERMUM L. Spec. Pl. 220. 1753.

var. ACUTIFOLIUM (Sm.) Gaudin Fl. Helvet. 2:259. 1828.—Inflorescence ± pyramidal, elongated.

var. OBTUSIFOLIUM Gaudin, l.c.—Inflorescence cymose, axillary, ebracteate. Upper leaves obtuse or mucronate.

According to Standley in N. Am. Fl. 21:13. 1916: "sparsely adventive in the United States from Maine to New Jersey and Tennessee, and in Oregon."

Subsection. 4. GROSSEFOVEATA Aellen et Iljin in Fl. URSS. 6:55. 1936. —Seed surface normally with round or elongated grooves and lacerated, broad margins but without radial ridges. Leaves deeply sinuate-dentate, with cordate base. Inflorescences terminal, pyramidal, ebracteate.

KEY TO SUBSECTION GROSSEFOVEATA

1. Grooves quite distinct ..... 61. *Ch. hybridum*
1. Grooves indistinct, shallow, irregular or almost wanting ..... 62. *Ch. gigantospermum*

61. CHENOPODIUM HYBRIDUM L. Spec. Pl. 219. 1753.
Not yet recorded from America.

62. CHENOPODIUM GIGANTOSPERMUM Aellen in Fedde Rep. spec. nov. 26:147. 1929.—*Ch. hybridum* of American authors, not of Linnaeus.

Canada: British Columbia, Alberta, Manitoba, Ontario, Quebec. United States: from Washington to California, Texas, Virginia, New York and Connecticut.

var. **typicum** Aellen, var. nov.—Semen 1.5-2 mm. in diam. latum. Pericarpium adhaerens. Perianthii laciniae lanceolatae vel oblongo-ovatae.

f. **cymosum** Aellen, comb. nov.—*Ch. gigantospermum* f. *cymosum* in Fedde Rep. spec. nov. 26:147. 1929.—Inflorescence cymose.

f. **spicatiforme** Aellen, comb. nov.—*Ch. gigantospermum* f. *spicatiforme* Aellen, l.c.—Inflorescence spicate.

f. **Griffithsii** Aellen, comb. nov. *Ch. gigantospermum* f. *Griffithsii* Aellen, l.c.—Inflorescence short, turning red.

var. STANDLEYANUM Aellen, l.c.—Seed large, to 3 mm. Pericarp not strongly adhering. Perianth tips broader.

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The Generic Name Auricularia

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The commonest auriculariaceous fungus in temperate North America is a species to which at least twelve binomials have been applied since 1821, of which the best-known are *Auricularia Auricula-Judae* (Fries) Schroet. and *Hirneola Auricula-Judae* (Fries) Berk. None of the twelve appears to be valid and the citations given for the various names are extremely erratic. So far as collections from temperate North America are concerned, there is, in most cases, little doubt as to the identity of the species involved. The same names, however, have been applied to numerous tropical collections, most of which certainly, and all of which possibly should be referred to other species. An investigation of the tropical species has led to the conviction that the nomenclature of the common temperature species should be revised, the genus itself properly validated and the desirability of the segregation of *Hirneola* be considered. Such a study will serve as an excellent case history to illustrate the difficulties inherent in the multiple starting-point provision for fungi in the present International Rules and the uncertainty induced by the vagueness in the wording of the clauses concerned.

It will be recalled that according to Article 20 (f) of the Rules, the nomenclature of the "Fungi caeteri," that is, all fungi except the Myxomycetes, lichens, rusts, smuts and gasteromycetes, begins with Fries's *Systema Mycologicum,* 1821-'32. As is well known, the *Systema* was issued in five parts, as follows: volume 1, 1821; volume 2, part 1, 1822: volume 2, part 2, 1823; volume 3, part 1, 1829; volume 3, part 2, 1832. In addition, the *Elenchus Fungorum,* embodying corrections and additions to the first two volumes of the *Systema,* indexed with them in the general index at the end of the third volume, and rightly regarded as a part of the *Systema,* was issued in two parts, both dated 1828. Whether these were issued simultaneously or separately is not clear, but assuming they were issued together, there are six publication dates for different parts of the work designated as the starting point for the nomenclature of the great majority of fungi.

The uncertainty referred to is brought about by the manner of citation of the dates and by the difficulty of ascertaining just what is meant by the word "group." What is a "group?" Is it a genus, a family, or one of the larger assemblages commonly recognized at the present time but only very roughly homologous with similar comprehensive assemblages accepted over a century ago? Are the dates 1821-'32 to be interpreted as inserted merely to give precision to the citation of the *Systema?* If so, is it thereby implied that all fungi included under the phrase "Fungi caeteri" constitute a single "group" for the purposes indicated in the article and hence with nomenclature starting

in 1821? Or does the citation of these dates imply that the categories of Fries must be perpetuated so far as possible and hence that each modern group—sometimes an order, sometimes a family, sometimes a genus—must have as its starting point that part of the *Systema* which includes the greatest number of recognizable species now embraced within it? The latter viewpoint has been generally accepted, sometimes explicitly, more often tacitly, and it may have been what was intended by some of those who framed the rule, but the actual wording does not demand it, and, in practise, as the taxonomic treatment departs more and more from the system followed by Fries, such an interpretation becomes more and more unworkable. C. W. Dodge (Ann. Missouri Bot. Gard. 21:709. 1934) proposed the amendment of Article 20 (f) by striking out "-32." Had this action been taken by the Amsterdam Congress, many of the difficulties suggested would have ceased to exist, but the Congress did not see fit to adopt the proposal.

On page 2 of the first volume of the *Systema* (1821), Fries lists *Auricularia* as a genus of his order Tremellinae. In the same volume he includes, in various genera, several tremellaceous fungi. In the special treatment of the Tremellinae, in the first part of the second volume (1822), it is made clear that the order, as envisioned by Fries, was based solely on the gelatinous consistency of the fructification and hence embraced not only tremellaceous fungi in the modern sense, but quite unrelated forms, such as the species included under *Coryne,* which he treats as a section of *Tremella. Auricularia* is not mentioned in this volume, but a description of *Exidia Auricula Judae* is given (p. 221) and in the Elenchus (1:154. 1828) of *?Phlebia mesenterica,* one of the synonyms of which is cited as *Auricularia mesenterica* Pers. The former species is the source of the combination *Auricularia Auricula-Judae,* although it has been questioned whether Fries's name applied to an *Auricularia.* Donk (Bull. Bot. Gard. Buitenzorg III. 17:161. 1941) believes it referred to a form of *Exidia truncata,* Fries's fourth species. Three years later, however, in another work (Syst. Orb. Veg. 82. 1825), Fries recognized *Auricularia* as a genus, indicating *A. reflexa* Bull. as the type and citing figures of Bulliard and Sowerby which clearly represent what is now known as *Stereum hirsutum. Auricularia* is not recognized in the later parts of the *Systema,* but in the index to the completed work, appearing in 1832, Fries lists thirty-nine species referred to *Auricularia* by earlier or contemporary authors and cited by him as synonyms, all referring to fungi characterized by more or less ear-shaped fructifications, with the footnote: "Genus reformatum est restituendum." Meanwhile, Fries had based the genus *Laschia* (Linnaea 5:533. 1830) on *L. delicata,* a tropical auriculariaceous species now commonly referred to *Auricularia* or *Hirneola.*

Shortly after the appearance of the first volume of the *Systema,* S. F. Gray (Nat. Arr. Brit. Pl. 1:593. 1821) adopted Nees von Esenbeck's genus *Gyraria,* roughly corresponding to the genus *Tremella* of Fries as published in 1822. His seventh species, *G. auricularis,* appears certainly to be what is now known as *Auricularia Auricula-Judae.* The following year, Persoon (Myc.

Eur. 1:97. 1822) recognized *Auricularia* and restricted it to two species, *A. mesenterica* and *A. Sambuci* (i. e., *auricularis* of Gray), hence *Auricularia,* in the modern sense, must be attributed to Persoon. Four years later, Wahlenberg (Fl. Suec. 2:993. 1826) used the name *Auricularia Judae* for what is clearly intended to be the species called by Fries *Exidia Auricula Judae.* His comment, "supra tantum fructificans papillis duriusculis" provides further evidence that this was an *Exidia,* as were the two species placed with it in *Auricularia.* In 1833, Link (Handb. 3:338) and Secretan (Mycogr. Suisse 3:228) recognized *Auricularia* in Persoon's sense, including in it what appear to be the same two species, under different names. What the sequence of publication of these two works was is not clear.

Persoon's treatment appeared after the first volume of the *Systema* but before the publication of the first part of the second volume. If the appearance of the latter work marks the starting point of the nomenclature of all tremellaceous fungi except those inadvertently described in the first volume, then *Auricularia* Pers. 1822 is pre-Friesian and invalid and *Auricularia* Fries 1825 is a synonym of *Stereum* Pers. ex S. F. Gray 1821. *Stereum* Fries 1825 applies to what is now known as *Hymenochaete* and *Laschia* Fries 1830 is the valid name for the species now referred to *Auricularia* and *Hirneola.* In order to avoid the changes which seem to be demanded by strict adherence to the rules, as commonly interpreted, Donk (l. c., p. 163) has recently proposed the conservation of *Auricularia* Secretan 1833 against earlier applications of the name. Donk's proposal is weakened by several factors. He assumes, incorrectly, that Gray's work appeared before the first volume of the *Systema;* he dates the first part of the second volume of the *Systema* 1823 and he ignores the publications of Wahlenberg and Link, the former certainly and the latter possibly earlier than that of Secretan. Moreover, the proposal to use Secretan's work to validate *Auricularia* against earlier applications of the name is peculiarly unfortunate. Secretan's citations are frequently inaccurate, he uses numerous trinomials and he actually prints the name of his second species *Auricula Judae,* although it may be inferred that *Auricularia* was left out in error. A much simpler and more practical solution is to agree to interpret the ambiguous word "group" in Article 20 as referring to all fungi in each category mentioned. If this were to be done, the starting point of the "Fungi caeteri" of 20 (f), including all not provided for elsewhere, would be 1821, as contemplated by Dodge's proposal. There might, however, be legitimate objection to this on the part of those who are concerned with the pyrenomycete orders. But it is difficult to see what there is in the rules to preclude interpreting "group" to mean Hymenomycetes, in Fries's sense, in which case 1821 will still be the starting place for *Auricularia.*

The first mention of *Hirneola* appears to be in Fries's *Systema Orbis Vegetabilis* of 1825, where it is listed on p. 93 and reference is made to Syst. Myc. 2:161, on which page *Peziza flava* Sw. (Fl. Ind. Occid. 3:1939. 1806) is put under the heading "Genus inquirendum." Farlow (Bibl. Index 304. 1905) recognizes this reference as publication of the combination *Hirneola*

flava [Sw.] Fries, although it is not actually printed. *Peziza flava* Sw. is, however, supposed to be the type of *Mycobonia,* in spite of the fact that Swartz clearly implies that it was growing on the ground, which is inapplicable to either *Auricularia* or *Mycobonia.* In 1849, in the Fungi Natalenses (K. Vet.-Akad. Handl. 1848:144), Fries redefined *Hirneola,* describing two new species and transferring twelve others to the genus, this time designating *Peziza nigra* Sw. (Fl. Ind. Occid. 3:1938. 1806) as the type. In the work cited, Swartz called the species *P. nigricans* and gave its habitat as "ad terram." In an earlier work, which I have not seen, he is said to have called the species *P. nigrescens.* In this description, Fries states that the hymenium of *Hirneola* is superior, an error copied by many later authors, appearing in Bresadola's work as late as 1932 and even used in keys to distinguish it from *Auricularia.* Because of the gelatinous texture of these fungi, the hymenium may at times be forced into a more or less superior position by the swelling of the substance, particularly when the basidiocarps are densely clustered, but morphologically it is nearly always inferior. The few well-authenticated exceptions may reasonably be explained on the basis of a disturbance of the substratum after the fructification had started to develop. Fries notes that no species of *Hirneola,* as defined in 1849, occurs in northern Europe. In another work published the same year but evidently written somewhat later (Summa Veg. Scand. 340. 1849), he suggests that most of the extra-European species of *Exidia* which had then recently been described were to be referred to *Hirneola.* The genus was accepted by Montagne, Berkeley, Saccardo and Bresadola and has been used by many recent authors. It was not recognized by de Bary, Brefeld nor Patouillard, nor by Lloyd in his later writings, nor by Lindau in the first edition of Engler and Prantl but was restored by Killermann in the second edition.

It is my contention that the word "group" in Article 20 (f) may reasonably be interpreted to mean something not less narrow than the Hymenomycetes of Fries. The genus name *Auricularia* is particularly indicated on page 2 of the first volume of the *Systema* as included in the order Tremellinae. Since, however, Fries seems to have been quite uncertain as to its character and limitations, the unmistakable reference of Persoon the following year (Myc. Eur. 1:97) should be taken as its starting point. *A. mesenterica* must be the type species. Not only is it the first of the two species listed, but the other species, *A. Sambuci* (i. e., *A. Auricula-Judae* of current usage) would have to be referred to what is now known as *Hirneola* by those who feel that a separate genus is justified. Both *Auricularia* and *Hirneola,* as typified by *H. nigricans,* have a tough-gelatinous hymenium composed of thickly-compacted, transversely 3-septate basidia immersed in gelatinized, forking paraphyses, the whole forming an extremely tough, almost rubbery layer when moist. *A. mesenterica* and *A. peltata* are characterized by a thick, fleshy-fibrous upper layer of the pileus which does not shrink greatly in drying, hence the hymenophores, when dry, have much the appearance of familiar species of *Stereum.* In those species often referred to *Hirneola,* this fibrous layer is much reduced, sometimes to a delicate layer of hairs, but more often forming a clearly per-

ceptible and sometimes dense tomentum. The degree of development of this layer may vary greatly in the same species at different ages or when developing in different environments. The distinction is clearly one of degree, not of kind, and does not deserve to be recognized by generic segregation. Nevertheless, for those who choose to make such a distinction, the genus *Laschia* is available. *Hirneola* Fries 1849 can be used only if it is conserved against both *Hirneola* Fries 1825 and *Laschia* Fries 1830. It seems unlikely that there are any informed mycologists at the present time who would go so far as to advocate the distribution of these fungi amongst three genera.

In order to summarize this discussion, the following citations and a generic description may be given:

AURICULARIA Pers. Myc. Eur. 1:97. 1822.

Laschia Fries, Linnaea **5**: 533. 1830; *Hirneola* Fries, K. Vet.-Akad. Handl. **1848**: 144. 1849; *Auricula* Batt. ex Kuntze, Rev. Gen. **2**: 844. 1891; *Patila* Adans. ex Kuntze, Rev. Gen. **2**: 864. 1891. Not *Hirneola* Fries, Syst. Orb. Veg. 93. 1825.

Fructification pileate, varying from nearly resupinate with slightly free margins to expanded applanate or auriform and substipitate or rarely stipitate, tough-gelatinous when wet, horny and brittle when dry; free portion of pileus always of two layers, an upper, scarcely gelatinous, sometimes coriaceous layer bearing hairs and varying from very thin to as thick as the lower portion and a gelatinous, or rarely subarid layer bearing the hymenium on the inferior surface; hymenium dense, composed of cylindrical, eventually transversely 3-septate basidia, with epibasidia arising from each basidial cell, and slender, branched paraphyses, the latter usually strongly metamorphosed, the whole covered by a tough surface membrane which is penetrated by the sterigmata; spores cylindrical or allantoid, germinating by a germ-tube, by the production of conidia or by repetition.

Type species: *Thelophore mesenterica* Bolt.

The common species of temperate North America is that listed as *Gyraria auricularis* by S. F. Gray in 1821. The synonymy, so far as I have been able to feel reasonably convinced of its correctness, is presented below. Karsten's Flora von Deutschland, cited by Bresadola without date, is not listed in any of the available bibliographies. Some additional pre-Friesian names have doubtless been employed since 1821. Other supposed and possible synonyms are given by Barrett (Mycologia 2:12-14. 1910). Insofar as these are based on tropical material, for example, *Auricularia ampla* Pers. and the combinations derived from it, they are extremely dubious.

Auricularia auricularis (S. F. Gray) comb. nov.

Gyraria auricularis S. F. Gray, Nat. Arr. Brit. Pl. **1**: 94. 1821; *Auricularia Sambuci* Pers. Myc. Eur. **1**: 97. 1822; *?Exidia Auricula Judae* Fries, Syst. Myc. **2**:

221. 1822; *Tremella Auricula Judae* Schw. Schr. Naturf. Ges. Leipzig **1**: 115. 1822; ?*Auricularia Judae* Wahlenb. Fl. Suec. **2**: 993. 1826 (the fungus to which Wahlenberg gives this name is, as previously noted, probably an *Exidia*, but the same combination used by Link (Handb. **3**: 338. 1833), without citing Wahlenberg, is probably the present species); [*Auricularia*] *Auricula Judae* Secr. Mycog. Suisse **3**: 229. 1833; *Exidia Auricula* Wallr. Fl. Crypt. Germ. **2**:559. 1833 (not seen; cited by Barrett); *Hirneola Auricula-Judae* Berk. Outl. Brit. Fung. 289. 1860; *Auricularia Sambucina* Mart. ex Winter & Demet. Hedwigia **24**: 185. 1885; *Auricularia Auricula-Judae* (Fries) Schroet. Krypt.-Fl. Schles. **3**:386. 1888; *Auricula Judae* Kuntze, Rev. Gen. **2**: 844. 1891; *Auricularia Auricula* [L.] Underw. Mem. Torrey Club **12**: 15. 1902; *Hirneola Auricula* [L.] Karst. Fl. Deutschl. 93 ex Bres. Icones Mycol. **23**, pl. 1109. 1932.

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Pre-Cambrian and Early Paleozoic Algae

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Algae of Pre-Cambrian and early Paleozoic (Cambrian and Ordovician) formations present problems that range from recognition of their organic origin to nomenclature, and from preservation or loss of microstructure to the interpretation of polyspecific complexes and their role in sedimentation.

This paper undertakes to survey these problems and contribute to their solution, as well as to suggest possibilities for future investigation. It also seeks to supplement the summaries of information upon early algae published by Pia (1927) and Seward (1931), stressing more recent discoveries and others whose full importance is not indicated by those authors. A large part of the paper is devoted to stromatolites, which outrank all other Pre-Silurian plant fossils in abundance, variety and importance as rock-builders. Sections devoted to the origin and naming of these structures, and their possible value as index fossils, are frankly controversial in form. No other treatment seems to be consistent with the need for answering objections and disproving conclusions which the writer deems unsound.

References are limited to papers bearing directly upon the topics discussed. It has seemed best to omit purely taxonomic papers and original descriptions when later papers provide more information and more significant illustrations.

Cells, Filaments and Films

Pia (1927, pp. 34-35) and Seward (1931, pp. 105-106) have reviewed early non-calcareous algae that possess distinctly preserved cells, filaments and sheaths. Simplest of these is *Gloeocapsomorpha* (Zalessky 1918 and earlier papers) from Ordovician argillites of Esthonia, deposits which are said by Seward to contain marine animals. *Gloeocapsomorpha* consists of minute yellow bodies .01 to .08 mm long, each containing several distinct cell groups in a mucilaginous matrix. The resemblance of photomicrographs to the modern *Gloeocapsa* is striking and probably significant, though Pia assigns the fossil form to Lindenbein's noncommittal Protophyceae.

Quite as obviously algal are cells, both isolated and in filaments, from the Archean (Gruner 1923, 1925), the Proterozoic Biwabik series of Minnesota (Gruner 1922) and the supposedly pre-Cambrian Kundelungu series of Rhodesia (Ashley 1937). The first consists of minute tubes which show more plainly in a slide than in photographs; Miss Tilden considers that they "resemble very closely" certain filamentous Cyanophyceae. The Biwabik algae, checked by Tilden, Rosendahl and Butters, are preserved in chert which contains well-preserved bacteria recognized by Henrici; one alga looks much like

the modern *Microcoleus*. Miss Tilden compared Ashley's Kundelungu filaments with the living iron-secreting *Lyngbya ochracea*.

Sederholm (1910, 1925) has described a bladderlike carbonized structure from the Pre-Cambrian of Finland as *Corycinium enigmaticum*. His figures, and those of a similar structure illustrated by Seward (1931, p. 91), suggest a tough-coated mass similar to those built by modern colonies of *Aphanocapsa* and *Nostoc*.

The most widely known and most convincing algal carbonaceous films are those of the middle Cambrian near Field, British Columbia (Walcott 1919). The genus *Morania* also resembles *Nostoc;* the genotype contains filaments and small balls of pyrite which seem to represent cells. Only one species, *M.* (?) *frondosa* Walcott is open to serious question as a cyanophyte; its large size and expanded films suggest a brown alga, perhaps an early laminarian.

Marpolia closely resembles the modern *Schizothrix* (Walton 1923) and is placed in the family Oscillatoriaceae by Pia (1927, p. 35). No significant opinion can be offered upon the position of *Waputikia, Yuknessia, Dalyia, Wahpia* and *Bosworthia,* though their shapes are consistent with Walcott's supposition that they belong to the Rhodophyceae. At least, they clearly are many-celled algae.

Carbonaceous films seem not to have been reported from lower Cambrian strata, though dark markings in micaceous, argillaceous quartzites of the Mount Whyte near Ross Lake, British Columbia, may be of algal origin. A small *Nostoc*-like form, *Morania antiqua* Fenton and Fenton (1937, p. 1950) is common in the middle Altyn formation of the Belt series in northwestern Montana.

Beltina, described by Walcott (1899, p. 338) as an arthropod, almost certainly is a brown alga.[1] This opinion was first published by White (1929a, p. 393) and is supported by specimens which are plentiful in the Altyn of Glacier National Park, Montana, and adjacent portions of Alberta (Fenton and Fenton 1937, p. 1949). They are fragments with indefinite shape and broken, irregular edges; films which at first glance seem to be jointed prove to be elongate fragments crossed by breaks or gaps that antedate fossilization. They closely resemble pieces of the brown algae *Fucus* and *Ascophyllum* mixed with broken shells on a tidal flat near Friday Harbor, Washington. Some of these pieces were partly buried in plastic, muddy sand, in attitudes suggesting the pebbles of edgewise breccias.

Carbonaceous algae from Ordovician strata have been described by Hall (1847), Whitfield (1894), Ruedemann (1909, 1912, 1925, 1934), Høeg (1926, 1937) and other authors. Though some of Hall's species have been removed from the algae, there remain a substantial number of forms which apparently belong to the Cyanophyceae, Chlorophyceae and Rhodophyceae.

[1] Raymond (1935, p. 382) tentatively accepts this interpretation, but says that a supposed *Beltina* from the Altyn of Glacier National Park (Walcott in Willis 1902, p. 317) is a fragment of an arthropod. The writer has not seen this specimen.

One of the most convincing of these is *Callisphenus gracilis* Høeg from the Wenlock of Sweden, a non-calcareous dasyclad. *Sphenophycus latifolius* (Hall) apparently is a brown alga with well-formed air bladders.

Laminae and Impressions

Carbonaceous layers and laminae are abundant in many formations. Some doubtless were produced by settling plankton or accumulation of dead organisms that drifted or rolled along sea bottoms. Others, however, apparently covered the sea floor with a tough but flexible mat that was capable of bending

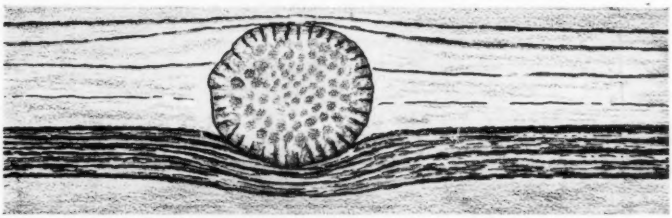

Fig. 1. Rhythmically laminated carbonaceous layer bent downward and compressed under a fallen *Favosites*. Traverse formation, west of Petoskey, Michigan. x 0.5.

Fig. 2. Laminated carbonaceous layers in gray middle Cambrian limestone near Yoho Pass, British Columbia. The carbon is attributed to mats of benthonic algae; minor rhythms may be seasonal.

under fallen corals and other massive remains. Such deposits range from a fraction of a millimeter to a centimeter or more in thickness; they commonly consist of rhythmic laminae in which carbon-rich sediment alternates with laminae poor in carbon. The layer illustrated in Fig. 1 is barely 3 feet in width and thins marginally, but those shown in Fig. 2 extend for many rods before they are hidden by talus.

Such accumulations suggest the algal sheets or mats described by Black (1933, p. 171) from Andros Island, in the Bahamas. The Andros colonies grow during seasons of reduced inorganic deposition; when sediment becomes abundant it kills all or most of the algae and the cycle then is repeated.

More spectacular, yet often less convincing, are impressions of the type known as *Rivularites*. As described by White (1929, p. 41) *Rivularites* is the impression of a colonial alga resembling the modern blue-green *Rivularia*. The thallus apparently possessed a tough basal carpet from which extended strands that floated in rapidly moving water. There may have been rhizoid holdfasts, but they could not prevent drag deformation of the basal carpet.

White's *R. permiensis* is a freshwater form occupying the bottoms of arroyos in which silt of the Permian Hermit Shale was deposited. Comparable impressions are found in micaceous, sandy shales between argillaceous quartzites of the lower Cambrian Lake Louise formation in Banff National Park, Alberta. Unfortunately, waters of the Lake Louise embayment were affected by waves rather than currents, at least during times of shale deposition. As a result, the supposed algae were deformed in ripple patterns and their borders were not distinctly marked. In fact, it is not possible to say with assurance that the markings are impressions of thalli, rather than atypical ripple marks.

This is equally true of markings scattered through some 200 feet of arenaceous and micaceous shale in the upper Cambrian of the Teton Range (Fenton and Fenton 1939, p. 98), although this member has been termed the Rivularites zone. Markings are of three general types, one of which is illustrated in Fig. 3, and all seem to grade into ripple marks. Channels delimiting supposed thalli are lacking.

Some authors have regarded *Kinneyia* (Walcott 1914, p. 107) as either ripple marks or impressions comparable to *Rivularites*. But exposure at the type locality show it to be nothing more than a dimunitive *Copperia* or *Greysonia*. All are inorganic: oblique or horizontal structures produced by segregation of calcite and dolomite during deformation of the Beltian Newland formation near the Big Belt Mountains of Montana (Fenton and Fenton 1936, pp. 612-615). The structures named by Walcott grade into flattened nodules, contorted masses and club-shaped forms, and are associated with columns of shallow cone-in-cone.

There is no need to review such fossils as *Cruziana, Rusophycus* and *Arthrophycus*. Although once considered plants, they are now known to be deep trails, burrows and other markings made by animals, especially arthropods

and annelids. Their animal origins are well shown by the illustrations of Hall (1852) and Delgado (1886; 1888).

Very different is *Oldhamia* (*Murchisonites*) *occidens* Walcott, of which impressions are found in lower Cambrian quartzites and slaty shales of New York. The writer has examined specimens collected and studied by Ruedemann (1925, p. 210; 1929) and shares his opinion that they represent algae. Their form, radial branching and indistinctly articulated structure, which shows more plainly in the fossils than in illustrations, indicates that they are small green algae comparable to the living *Halimeda*. This alga is commonly cast upon beach sands and sandy muds; if buried it is soon dissolved by carbon dioxide from decayed organic matter. The impressions left by stranded specimens are remarkably like the more distinctly articulated examples of *Oldhamia*. It is not clear whether the appearance of *O. occidens* as "a series of whorls . . . so closely arranged that the bases are not shown" is a character of growth or of deposition. Ruedemann accepts it as the former, but one of his figures (1929, p. 47) resembles the irregular series of *Halimeda* stocks which commonly are left on gently sloping beaches. Their arrangement apparently is determined by retreating waves whose waters move as is indicated in Fig. 4. "Stalks" connecting whorls or fanlike stocks in *O. antiqua* Forbes (Ruedemann 1929, p. 49) seem to be diagrammatically drawn rill marks like those seen to extend from the bases of stranded *Halimeda* stocks.

Fig. 3. Supposed *Rivularites* impression in upper Cambrian shale of the Teton Range near the head of Death Canyon, Grand Teton National Park, Wyoming.

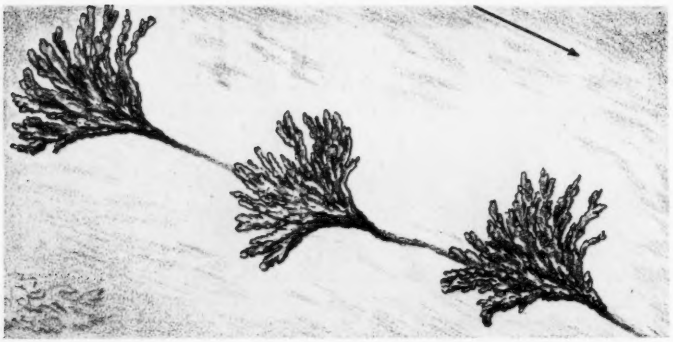

Fig. 4. Sketch of three stocks of *Halimeda* stranded upon a beach north of Cape Perpetua, Oregon. Rill marks from the base of each stock would give the appearance of a continuous stem in a fossil impression or filling. Arrow shows direction of movement of the receding waves.

Calcareous Green Algae

If *Oldhamia* is correctly interpreted in the preceding paragraph, it is the oldest known member of the calcareous Chlorophyceae and may be placed provisionally in the family Codiaceae, which contains *Halimeda*. Another ancient member of this family is the tubular *Palaeoporella*, whose branches form limestones in the Baltic region (Stolley 1897; Hadding 1933, p. 21). The genus appears in Cambrian strata and reaches its greatest development in the lower Ordovician.

Pia (1927, pp. 61-86) has reviewed the Dasycladaceae, of which at least ten genera are found in the Ordovician. They include the American forms *Cyclocrinus* (including *Pasceolus* and *Cerionites*), *Mastopora* and *Primicorallina*. Ruedemann (1909, p. 200) thinks that *Primicorallina* is important in granular and oolitic limestones of the Trenton; he records a member at Glens Falls, N. Y., whose grains "quite certainly are derived from calcareous algae." The writer found lenses of similar material in Plattin limestones of Ste. Genevieve County, Missouri, though the grains were too large to be attributed to *Primicorallina*.

The problem presented by calcareous Chlorophyceae in North America is primarily one of discovery. This depends partly upon recognition of compressed or beadlike granules showing the form or structure of algal segments. Less difficult will be the recognition of cylindrical or barrel-shaped tubes of such forms as *Palaeoporella*. It is desirable, also, to seek forms resembling *Oldhamia* and to establish characteristics by which they may be separated from radial annelid burrows.[2]

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2 Neither this suggestion nor discussion in the preceding section overlooks the fact that several paleobotanists have rejected *Oldhamia* on the ground that it is inorganic. But as Ruedemann (1929, pp. 49-50) points out, their criticisms apply chiefly to *O. radiata* Forbes, which differs radically from the fanlike forms here compared with *Halimeda*.

Digitate, Branched and Tubular Red Algae

Although *Solenopora* appears in lower Ordovician strata and is abundant in the Silurian of northern Europe, there is a widespread opinion that the Rhodophyceae played a minor role during the Pre-Cambrian and early Paleozoic. Yet they seem to have been responsible for great thicknesses of mottled or "fucoidal" dolomites. As will be indicated later, they may also have been important in the formation of stromatolitic algal deposits, as well as in layers and laminae generally attributed to inorganic sedimentation.

The most important contribution to our knowledge of problematic rhodophytes of the early Paleozoic was made by Blackwelder (1913), who emphasized the dichotomous branching of resistant, highly magnesian structures that characterize the Ordovician Bighorn formation of Wyoming. He compared them with modern rhodophytes, concluding that "the modern coralline algae seem to fill the requirements of the case for the Bighorn dolomite. . . . Therefore it appears to me probable that the peculiar features of the Bighorn dolomite are of organic origin, and that the more massive coralline algae, such as . . . *Lithophyllum*, may fairly be regarded as competent to make such structures, if indeed they are not the only organisms which could have done so." (p. 618)

Fig. 5. Supposed red algae in the Ordovician Bighorn dolomite. Beartooth Butte, east of Cook, Montana.

The fact that supposed coralline remains in the Bighorn preserve no trace of internal structure presents no serious difficulty. Walther (1885; 1919, p. 181) and Seward (1894, pp. 19-20) have stressed the rapidity with which percolating waters destroy the structure of Lithothamnium and other calcareous red algae as well as "well-formed" corals. Moreover, as Blackwelder points out, the cells of modern Lithophylloids average about .01 mm in diameter, while crystalline grains in the Bighorn range from .05 to 1.0 mm. Thus the smallest rock particles are five times as large as average algal cells while the largest are a hundred times. Under such conditions preservation of algal microstructure is impossible.

The branched algal content of the Bighorn may be estimated at 30 to 40 per cent in beds which have much matrix and 60 to 80 per cent in strata whose algae are very closely packed. Much of the matrix apparently consists of algal sand, with a mixture of clay and apparently precipitated calcite. This composition is consistent with the nature of the Bighorn as a "comparatively pure" dolomite, for the coralline algae are highly magnesian, though stony Chlorophyceae such as *Halimeda* are almost free of magnesia (Clarke and Wheeler 1917, p. 44). Thus the nature of the rock agrees with Blackwelder's conclusion that its dominant constituents are corallines.

Structures much like those of the Bighorn and so distinct in shape that they can be used for short-distance correlation have been found in the middle

Fig. 6. Supposed red algae in the middle Cambrian Ptarmigan formation near Wenkchemna Pass, Banff National Park, Alberta.

Cambrian Cathedral and Ptarmigan formations of Banff and Yoho National Parks, in western Canada. Others appear in specimens of middle Cambrian "mottled" dolomite from the Cottonwood district of Utah, collected by F. C. Calkins. "Fucoidal" limestones and dolomites have been observed in the Ordovician Platteville, Kimmswick and Galena formations of Missouri and northeastern Iowa; the first of these contains structures described as *Buthotrephis brachiatus* (Fenton 1928, p. 126) which closely resemble the supposed corallines of the Bighorn. Both Kimmswick and Galena contain members which suggest the Bighorn in reverse, with matrix preserved and red algae removed by solution. Some of the resulting cavities contain very coarse dolomite grains, which suggest that destruction of the algae was caused by coarse crystallization that facilitated the action of ground water.

A surprise of field work in the Teton Mountains during 1936 was the discovery of tubular and irregularly expanded structures described as *Aulophycus* (Fenton and Fenton 1939, p. 104). Despite variations, the five recognized species exhibit definite zonation and do not intergrade. Some expanded phases of one form, *A. prolificus,* show indistinct laminae, but the great majority are without structure. They obviously are not dasyclads and are provisionally assigned to the Rhodophyceae—perhaps to a group now extinct.

Discovery of *Aulophycus* raises a question as to the nature of some Ordovician fossils referred to *Palaeophycus* (Hall 1847, p. 7). The genotype, *P. tubularis,* seems to be a burrow filling, but *P. simplex* Hall of the Trenton apparently is tubular and so may be related to *Aulophycus*. The same is true of *Manchuriophycus* (Endo 1933) from the Proterozoic Sinian series of southern Manchuria, though this genus shows interwoven filaments.

Are Stromatolites Organic?

The great majority of Pre-Cambrian, Cambrian and Ordovician algae belong to the forms variously known as stromatolites (Kalkowsky 1908, p. 68) or spongiostromes (Gürich 1906, p. 7), the former being preferable on grounds of implication and etymology (*stroma,* layer; *lithos,* stone). Though variations are almost endless, these structures may be grouped into three general types:

1. Nodular, columnar, spheroidal or biscuit-shaped forms made up of superimposed or concentric laminae which are gently curved to intensely crumpled. Some forms also show vesicular and radial or vertical structure. *Cryptozoon* Hall and *Collenia* Walcott are the best-known examples.

2. Laminar sheets, lenses and irregular expansions, some of which are extensions from stromatolites of Type 1, though others are distinct growths. Several members of this type have been *referred* to Collenia; others are unnamed.

3. Spongy or vesicular masses and sheets without distinct laminae. *Camasia* Walcott is typical.

The first and second types intergrade; the second and third probably do

so. The closest approach to intergradation between the first and third is provided by *Newlandia* Walcott and *Hadrophycus* Fenton and Fenton, both of which possess radial or vertical pillars and irregular to vesicular laminae.

Since they first attracted the attention of paleontologists, stromatolites have provoked uncertainty and disagreement. They were long regarded as animals—protozoans, stromatoporoids, sponges, corals—but were transferred to the plant kingdom by the work of such authors as Garwood (1913, 1913a), Walcott (1914) and Wieland (1914). Yet they were accepted with skepticism, and Holtedahl (1919, 1921) soon rejected many forms as inorganic. Seward (1931) went still further, pronouncing them "inorganic structures" and "artifacts."

Several authors have explained why stromatolites may not be relegated to the inorganic realm, yet opinions to that effect persistently reappear. It seems desirable, therefore, to summarize both criticisms and answers, and to follow this summary with a brief statement of the grounds on which those who work with stromatolites maintain that they are algal as well as organic.

1. *Criticism:* That many stromatolites are typical concretions whose laminae are comparable to Liesegang's rings.

This widely-held opinion has been restated by Seward (1931, pp. 86-88) who illustrates rings in silver chromate, apparently for comparison with *Cryptozoon proliferum* Hall. But as Goldring (1938, p. 21) remarks, there is no similarity between the regular, progressively widening rings and the laminae or layers of *Cryptozoon* and other stromatolites. The latter are variable in thickness and constitution; they are irregular and crumpled or unevenly curved; they commonly display rhythmically alternating mixtures of calcite, dolomite or chert with clay, carbon, siliceous sand and other substances. Nor do Liesegang's rings show any trace of the vesicular texture and radial or vertical pillars which characterize such stromatolites as *Camasia*, *Newlandia* and *Hadrophycus*.

Similar differences exist between undoubted concretions and stromatolites. Mrs. Fenton and I have compared several hundred stromatolites with concretions from strata which range from Beltian to Recent in age. Most of the concretions are laminated, while some show radial structures. But the laminae are utterly unlike those of stromatolites and the radial structures are either crack fillings or results of crystallization. We conclude that the supposed resemblance between undoubted concretions and stromatolites is too superficial to merit consideration.[3]

2. *Criticism:* That some stromatolites are identical with secondary structures produced by crystallization and other "radical internal changes in the rocks."

This conclusion was reached by Holtedahl (1921) and Seward (1931, p.

3 Emphasis is properly placed on *undoubted* concretions. Nothing can be gained by accepting at face value illustrations of "concretionary beds" or "concentrically laminated concretions" which actually portray stromatolites, and using them as evidence. Such illustrations are common in geologic literature.

89) from a comparison of structures in the Permian dolomite of County Durham, England, with Pre-Cambrian algae described by Walcott (1914). Holtedahl finds one type to be almost identical with *Newlandia* while another bears 'very striking" resemblance to Greysonia, and a third type resembling *Camasia* "should not be difficult" to find. *Copperia, Kinneyia, Collenia* and *Weedia* are not mentioned; for the last two Holtedahl has another possible explanation (Criticism 3).

Examination of Holtedahl's illustrations and several specimens supplied by the British Museum shows that the Permian structures are inorganic, but denies them further significance. The supposed *Newlandia* is a complicated cone-in-cone whose sections are crudely prismatic. As shown in Fig. 7, it bears only superficial resemblance to *Newlandia* and is not much like Walcott's dubious *Gallatinia* (1914, p. 116), which does contain structures suggesting cone-in-cone. The structures thought to resemble the non-laminate *Greysonia* are conspicuously laminated concretions or segregations of radically different character—and besides, *Greysonia* has been removed from the stromatolites (Fenton and Fenton 1936). The closest approach to *Camasia* among specimens examined is a complex mass of spheroidal concretions. In short, the Permian structures not only differ from Walcott's true stromatolites; they do not even resemble *Greysonia* and the related *Copperia* and *Kinneyia*, now known to be inorganic.

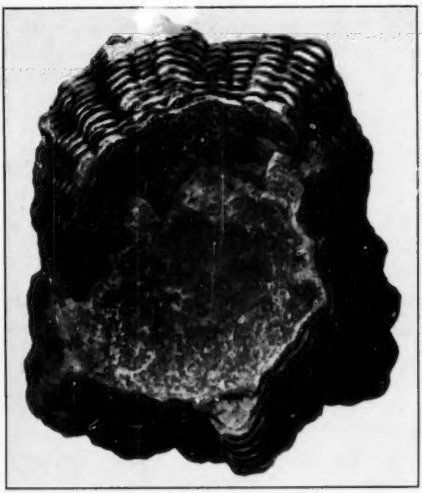

Fig. 7. Complex cone-in-cone structure from Permian dolomite of Sunderland, County Durham, England. This is the type which Holtedahl compared with the algal stromatolite *Newlandia* of Walcott.

3. *Criticism:* That many stromatolites are too indefinite in form and structure to be more than the results of chemical precipitation initiated by organisms but not controlled and given shape by them.

This opinion also was formulated by Holtedahl (1919, p. 96) and was directed especially against *Cryptozoon* and *Gymnosolen*. It is based upon their possession of laminated but not radial structure and the frequent inclusion of oolitic and clastic material. But such inclusions are common in colonial corals, while radial structure is pronounced in *Newlandia* and *Hadrophycus*. The remarkably stable characters of laminae and the structures which they form in three closely associated species of *Cryptozoon* (Goldring 1938) is a further argument against uncontrolled chemical precipitation.

Indeed, the absence of any special structure from supposed calcareous algae is very dubious evidence against their organic origin. The loss of structure from modern corallines has been mentioned; even laminae commonly are indistinct in travertines, tufas and "lake balls" formed by living Cyanophyceae. The massive Pre-Cambrian stromatolite *Hadrophycus* shows prominent pillars and weak laminae when preserved in amorphous chert, but no pillars and very distinct laminae when preserved in alternating layers of crystalline chert and dolomite (Fenton and Fenton 1938, p. 4; 1939, plates 2-3). A critic having only specimens of the second type might well voice Holtedahl's objection yet be in error as he did so.

The hypothesis of "chemical precipitates . . . that came into existence through the organic [photosynthetic?] processes of living" things might be applied with greater probability to such stromatolites as *Weedia* (Fenton and Fenton 1931, p. 686). Even this possibility is rendered doubtful by the fact that algae are known to build up layers of varied character, as will be shown under the heading of Rock Layers and Laminae.

4. *Criticism:* That stromatolites and other supposed algal fossils are to be rejected as inorganic unless they contain filaments and cells which demonstrably had a "share in the production of the enclosing matrix."

This, the most sweeping objection of all, was advanced by Seward (1931, p. 88). If followed literally, it would deny any significance to macrostructure and even to actual remains unless their action in production of laminae, pillars and other structures could be proved.

As Seward himself hints, this criticism is part of a "too-sceptical attitude" which defeats itself by its very insistence upon reliable evidence. The loss of microstructure in modern coralline algae has been mentioned, and equally rapid destruction takes place in deposits built by calcareous blue-greens. Tufas and travertines show only the crudest of laminar and vesicular structure and the central portions of "lake balls" are not much more distinct. Mawson (1929, p. 617), Howe (1932, pp. 59-60) and others have commented upon the lack of structural detail in such deposits and the difficulty of demonstrating algae in any except the most superficial layers of travertines and tufas in actual

process of deposition. Turning to *Cryptozoon* and other ancient stromatolites, Howe concludes that "In view of the extreme age of these supposed plants and the extreme delicacy of the gelatinous walls of the Myxophyceae Cyanophyceae, even when more or less calcified, it seems unreasonable to expect any preservation of their microscopic cell structure."

As we shall see, this "unreasonable expectation" seems to be fulfilled by a few specimens, though not with the detail Seward seems to demand. But no widespread discovery of filaments, tubes or cells in stromatolites can be anticipated, and nothing is to be gained by setting up an unattainable standard which, *a priori,* would remove the problem of problematic stony algae from scientific consideration. It seems much better to take what evidence can be found, use it as it can be used, and draw conclusions even though they may be subject to future disproof or revision.

The first of those conclusions must be that the inorganic origin of stromatolites is a hypothesis without present support,[4] but with an embarrassing record of discredited evidence. It plainly forms no obstacle to other interpretations.

Stromatolites as Algae

Every student of stromatolites will admit that their prevalent lack of detailed microstructure is a serious disadvantage to interpretation of these bodies. Yet there are several lines of evidence which indicate that stromatolites are both organic and algal, and suggest the major groups to which they belong. This evidence may be summarized as follows:

1. Where calcareous or dolomitic laminae in stromatolites can be correlated with those in enclosing strata, the former always are much thicker. (Fenton and Fenton 1937a, pp. 1932-1933). This shows localization of the agents which caused precipitation of the stromatolite laminae and gave them their characteristic shapes. Such localization apparently can be explained only by growth of organisms.

2. Many—perhaps most—stromatolites exhibit remarkable stability in both shape and macrostructure. This stability may be maintained through thick formations and over extensive areas, under varying conditions of sedimentation (Fenton and Fenton 1937, p. 1945 ff.). It is most conspicuous, however, where related yet distinct stromatolites exist in adjacent strata, as do *Cryptozoon proliferum* Hall and *C. ruedemanni* Rothpletz in the Hoyt of New York (Goldring 1938). Such stability is consistent with organic origin but not, so far as is now known, with inorganic.

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4 This statement does not overlook the fact that *Greysonia, Copperia* and *Kinneyia* of Walcott (1914) are products of segregation under the influence of pressure and deformation. They lack any trace of laminar structure and of vertical-columnar, radial or concentric growth. They could not be termed stromatolites, even before their inorganic nature was established. The significance of *Gallatinia,* which combines the shape of a stromatolite with what seems to be cone-in-cone in combined radial and circular arrangement, is too uncertain to be significant.

3. In spite of their fundamental stability, stromatolites show minor variations which are directly concerned with habitat and major variations which may be correlated with stratigraphic and sedimentary evidence of shallow water, wave action and other environmental factors. Such variations are known to be typical of corals, corallines and calcareous blue-green algal complexes.

4. Stromatolites form typical biostromes (beds) and bioherms (reefs). Such deposits have been built by known algae, as well as by corals, stromatoporoids, bryozoans and other animals. They have not been convincingly attributed to purely inorganic structures and processes.

5. As has been stated, both laminae and layers of stromatolites show variations in thickness, coarseness or fineness of grain, and amounts of such materials as carbon, clay and sand. They form domes and mammillae of characteristic shapes and sizes; they often run together or expand and separate with great complexity. The development of many was halted by substantial deposits of clay, edgewise breccia, oolite and other sediments. In all these respects they agree with deposits in living calcareous algae and with such undoubted algal structures as those formed by *Chlorellopsis coloniata* Reis of the Eocene (Bradley 1929) and *Oncobyrsella coloradensis* Johnson (1937) of the Oligocene. Many small stromatolites also resemble the cyanophyte *Girvanella,* in which microstructure is well preserved.

6. Spongy, or vesicular, stromatolites bear close resemblance to "lake balls" and similar deposits, known to be formed by blue-green algae (Walcott 1914, Mawson 1929, Howe 1932 and other authors).

7. At least one stromatolite, *Cryptozoon proliferum* Hall, possesses conceptacles in which apparent spore cases are preserved (Wieland 1914, pp. 241, 244); they suggest conceptacles of *Lithothamnium.* Stromatolites of the supposed Proterozoic iron-bearing formation of the Belcher Islands, in Hudson Bay contain iron oxide replacements 0.5 to 2.5 and 5 to 10 microns in size; to J. B. Hill they suggest the modern Coccogoneae and Hormogoneae (Moore 1918, p. 427).[5]

8. The concentration of heavy potassium on Saratoga mineral waters indicates that the "salt deposits from which the water arises are of marine plant origin," and so points toward the algal nature of *Cryptozoon* (Baudisch 1937, summarized by Goldring 1938, p. 31).

No single one of these lines of evidence is convincing, but the entire series justifies acceptance of stromatolites as structures of organic origin—as sheets, columns, domes and other masses built up by algae which precipitated calcium carbonate upon and around their thalli.

In the opinion of Howe (1932), Pia (1926, 1927) and most other workers,

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[5] The nature of small stromatolites containing these replacements is not obvious from Moore's figures. Larger masses up to 14 inches in diameter, which both Moore and Howe compared with *Cryptozoon,* resemble the massive, dome-shaped form of *Collenia symmetrica* F. and F. of the Beltian lower Siyeh formation.

those algae were members of the Cyanophyceae. But Wieland compared the conceptacles of *Cryptozoon* to those of a red coralline, *Lithothamnium* which is hemispherical to spherical in form. Miss Tilden (oral statement) suggests that many stromatolites were built up by red algae, and her opinion is consistent with the fact that large numbers of stromatolitic biostromes and bioherms are dolomitic. Without abundant microstructures, however, it seems impossible to determine the relative importance of Rhodophyceae and Cyanophyceae in these still problematic fossils.

Stromatolites Compared with Lahontan and Pyramid Tufas

Instructive comparisons may be made between ancient stromatolites and the calcareous deposits of Pleistocene Lake Lahontan, Nevada, as well as those now forming in Pyramid Lake, Lahontan's principal remnant. As described by Russell (1885) and Jones (1925), Lahontan tufas are calcareous—not dolomitic—deposits of three general types:

1. *Lithoid Tufa.* Laminar deposits of compact, stony texture. They cover volcanic rocks of the old lake shore, isolated cobbles or pebbles and other algal deposits, with which they commonly are interbedded. Some exposures exhibit tubular structures and others are slightly porous, but the majority show no structure other than indistinct laminae.

2. *Dendritic Tufa.* Coralloid or vesicular deposits that vary greatly in gross

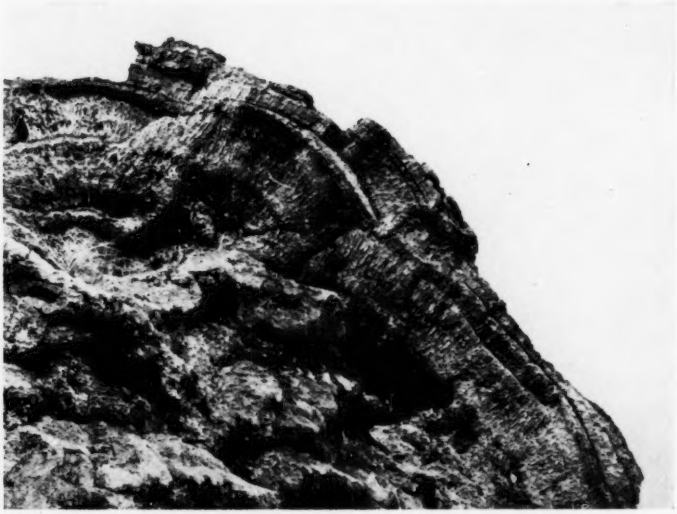

Fig. 8. Layers of thinolitic tufa over dendritic, with layers and laminae of compact lithoid tufa. Lahontan "domes," of biostromes, Sutcliffe, Nevada.

structure and form. Some suggest an exceedingly coarse *Camasia;* others consist of curved botryoidal layers or masses that spring from many separate centers. Where they are crowded, growths from these centers form rough prisms; those prisms that were outstripped by their neighbors end in points or pyramids. Other variants resemble the modern corallines *Lithophyllum* and *Goniolithon* but alternate with more massive deposits and mammillose lithoid sheets.

3. *Thinolitic Tufa.* Coarsely layered or banded deposits composed of interlaced crystals of thinolite, a form of calcium carbonate which began as aragonite. Thinolitic tufa covers volcanic rocks and lithoid sheets, and also forms thick bands in the larger and older dendritic domes, crags and tufa "castles."

There is a distinct zonation in these deposits, the lithoid rising highest upon the Lahontan shore line, the thinolitic being intermediate in position, and the dendroid extending to the present level of Pyramid Lake. Yet there also is extensive intermingling and intergradation between types. In general, the break between lithoid and dendritic is sharper than that between dendritic and thinolitic tufas, since dendritic crusts surround large thinolite crystals and fill many spaces between them.

Russell considered all three types to be chemical precipitates, but Jones (1925, p. 23) found well-preserved algal remains in both lithoid and dendritic deposits. He then turned his attention to the algae and tufas of present-day

Fig. 9. Algal tufa on basalt blocks and subangular cobbles of a Lahontan shore cliff near U.S. Highway 40, northeast of Fernley, Nevada. The base of the deposit is lithoid; the rest is dendritic tufa of the irregular, porous type.

Pyramid Lake. As seen in 1913 (Jones 1925, p. 9), the sequence begins with a fringe of green non-calcareous *Cladophora* about equally divided above and below water level. "Below this band a grayish-white alga, another species of *Cladophora,* . . . grew in tufts and bunches that had their bases so firmly fixed in the layer of recent tufa that pulling the algae from the rocks brought the tufa with them. At the base of the tufts was a narrow zone of blue-green algae that included species of *Calothrix, Nostoc,* and *Formidium.* On the under side of projecting rocks and older tufa the same blue-green algae were found growing in the absence of *Cladophora,* and with their bases firmly fixed in a thin film of calcareous deposit. Similarly, at depths of 4 feet and over, the blue-greens grew in the absence of the other algae, and in every instance in constant association with the recent tufa. It would seem that the blue-green algae require a somewhat diffused light and that they are unable to grow at or near the surface of the water unless protected and shaded from the direct sunlight by the other algae or the rocks."

Brief examination in 1941 and 1942 by Mrs. Fenton and myself brought out no features of algal distribution not noted by Jones. We did observe that tufa deposits are most evenly laminar and compact where the water is well-lighted and disturbed but are roughest and most porous in quiet, shaded situations.

No trace of thinolite has been found in Pyramid Lake, and Jones concludes

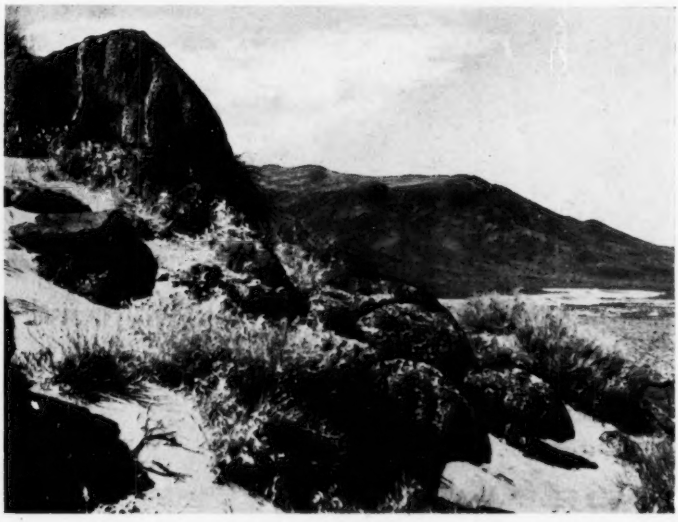

Fig. 10. Mushroom-shaped dendritic tufa which grew upon angular cobbles near the locality shown in Fig. 9, but about 20 feet below it. The cliff is partly covered with fine siliceous sand.

that it is an inorganic deposit formed at a time when Lake Lahontan was virtually saturated with calcium carbonate. Thinolitic tufa is most extensively developed on terraces and domes where waves must have splashed vigorously, but small crystals were produced experimentally in standing water. Jones emphasizes the fact that thinolite settled only upon older algal tufas, whether these formed domes, covered massive rocks, or made crusts on scattered pebbles.

For our purpose, two facts have special significance. One is that inorganic tufas differ radically from those of organic origin and can be distinguished even when the two intermingle. The other is that the two types of organic tufas differ in environmental relationships and apparently in the groups of algae by which they were produced.

Algal tufas of a shore northeast of Fernley, Nevada, were compared with those of the Beltian biostrome shown in Fig. 12. The uppermost Lahontan cliffs, in the zone of splashing waves, are covered with lithoid sheets comparable to the laminar stromatolites on the front and crest of the Beltian reef. Lower down and among loose blocks of rock are dendritic masses which find their counterpart in the conical ecad of *Collenia frequens* (Walcott) and the type designated Ecad B (Fenton and Fenton 1937a, p. 1946). Near the foot of the cliff, on banks of what once was compact limy mud, are scattered dendritic masses which resemble *Cryptozoon proliferum* Hall in shape. They

Fig. 11. Dendritic Lahontan algal tufa of the general shape shown by colonies of *Cryptozoon proliferum* Hall. Note peripheral dendritic growth with covering of lithoid tufa. Near foot of cliff shown in Fig. 10.

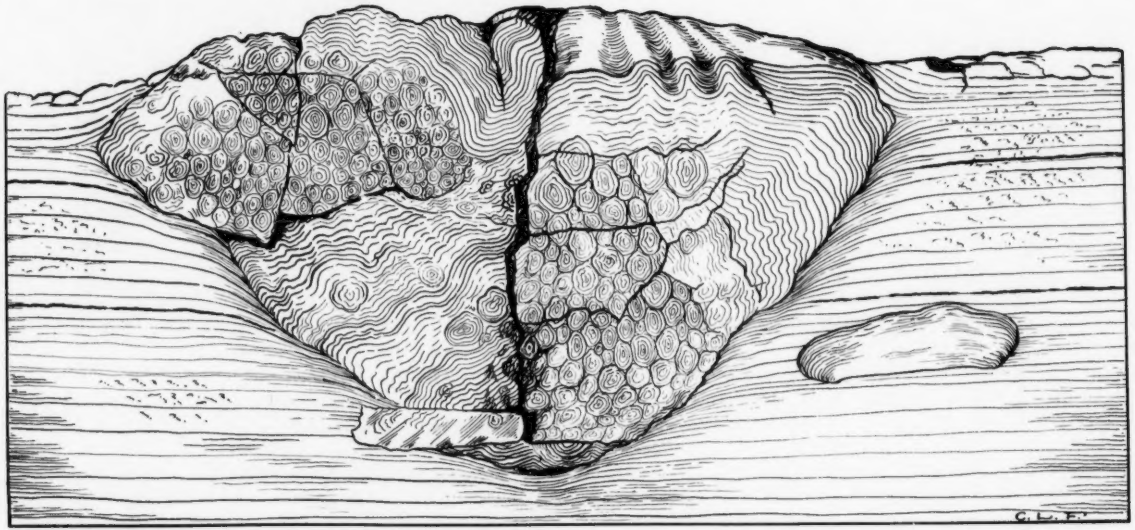

Fig. 12. Bioherm, or reef, of *Collenia frequens* Walcott in the Beltian Siyeh formation of Glacier National Park, Montana. Upper portion and fore-reef are formed by the laminar ecad called *C. compacta* by Walcott; the core and left portion consist of the conical ecad which probably is identical with *Conophyton* Maslov (1938) of the Asiatic Proterozoic and Cambrian. The isolated colony resembling Fig. 11 probably is *Collenia willisii* F. and F.

find their counterpart in the open-bottom ecad of *Collenia frequens,* as well as the depressed form of *C. willisii* Fenton and Fenton.

A comparable sequence appears in isolated tufa domes and "castles," which actually are biostromes. Here the core of the structure is made up of vase-shaped or spheroidal dendritic tufa often with an intermediate zone of thinolite, though this is lacking from most biostromes of the latest Lahontan stages. The upper and outer portions of dome-shaped biostromes and "castles" are dendritic, but both in section and upon the surface they show coatings of lithoid tufa. Depressed or spheroidal dendritic masses occupy platforms of tufaceous breccia around many biostromes. They are much more compact than the biscuit-shaped structures found upon former mud flats.

This difference may be significant in the interpretation of ancient stromatolites, for many of the most compact columnar or biscuit-shaped forms of *Cryptozoon* and *Collenia* are found in beds of coarse sediment that contain mudballs, cross-bedded oolites and edgewise breccias. On the other hand, such porous form-genera as *Camasia* and *Newlandia* appear in strata that show little trace of disturbed water.

Fig. 13. Upper surface of two very large compound colonies of *Collenia willisii* F. and F. from the upper Siyeh of Hole-in-the-Wall Cirque, Glacier National Park, Montana. Though formed by fusion of several colonies, these masses resemble that of Fig. 11 in general shape and probably in their habitat, though the latter was marine.

Rock Layers and Laminae

Lithoid tufas of Lahontan and Pyramid lakes show that algae can deposit stony layers upon hard rocks and apparently upon firm mud bottoms. Similar deposits, extending from columnar stromatolites, are shown by large natural sections of the Cambrian *Collenia spissa* Fenton and Fenton (1939, p. 101) and to a lesser extent by the supposed red alga *Aulophycus*.

Of more general significance are laminated, mottled or crudely vesicular layers of both dolomite and limestone found in many formations of the Pre-Cambrian and early Paleozoic. The first of these is conspicuous in the Beltian Siyeh (Fig. 12), especially in the member which contain algal biostromes. The layers show pronounced calcite-dolomite rhythms and bend downward beneath large algal masses. It is obvious that they were firm yet tough and flexible, remaining so for a long period after their deposition.

The obviously stromatolitic nature of layers extending from *C. spissa* led to a comparison with calcareous algal deposits studied by Tilden (1897), who already had concluded that similar rock layers in the Platteville of the upper Mississippi Valley were of algal origin (oral statement). The writer now shares this opinion and thinks it desirable to search for evidence of algal action in other thinly bedded limestones and dolomites. Such evidence may

Fig. 14. Crumbling "castle," or bioherm, of dendritic algal tufa near the southern end of Pyramid Lake, Nevada. Dome-shaped colonies occupy a platform at the base of this bioherm.

Fig. 15. Algal masses on the surface of a middle Cambrian slab near Ptarmigan Pass, Banff National Park, Alberta. Except for their small size (diameter 4-9 inches) they show general resemblance to Fig. 11. This slab contains marine animals.

never be convincing and it will not turn extensive layers into stromatolites, yet it may contribute to an understanding of their origin and lithologic features.

It may also provide a tentative explanation of limestone-dolomite rhythms such as those of the Siyeh. In a single tank, Miss Tilden found two kinds of deposits: a relatively smooth type containing *Dichothrix* and *Lyngbya* (cyanophytes) and a much rougher, irregularly mammillose type containing these genera plus the green alga *Chaetophora* (whose secretion of calcium carbonate is independent of that by the blue-greens) covering the substratum which they lay down. The contrast is ecologic, for *Chaetophora* is limited to quiet water while *Lyngbya* and *Dichothrix* thrive in either quiet or currents. Comparable contrasts in other assemblages depend upon light, temperature and depth of water.

The Belt sea was subject to a variety of fluctuations which ranged from seasonal variations in light to flooding and deposition of edgewise breccias (Fenton and Fenton 1937, pp. 1905 ff; 1929 ff). It seems reasonable to suppose that some of these rhythms encouraged the growth of calcareous (blue-green?) algae at one phase and magnesian (red?) algae at others.

Layers of one type are less problematic; as observed in the Plattin-Platteville and some other formations, they include only a depositional phase in which algae presumably were active and a non-depositional phase, in which they were not. Sediment therefore was small in amount and dominantly clastic. In northern seas this rhythm might well be seasonal, at least for thin deposits.

Naming Stromatolites

Analogy with modern algal deposits, especially those of the cyanophytes, indicates that each stromatolite is the product of several species or even genera of algae that lived in communal, if not symbiotic, association. This probability, plus the possibility that identical stromatolites may have been formed by different groups of organisms, has led such authors as Høeg (1929, p. 8) to conclude that stromatolites should not be named. This opinion has been seconded by Cloud (1942, pp. 364-366), who thinks paleontologists have knowingly committed many an impropriety in naming genera and species of these fossils. Cloud would replace specific names with descriptions like those used for textural characters of sedimentary rocks, but would keep a few generic designations for use in "a vernacular sense, without being italicized or capitalized."

Several answers may be made to these objections. The most obvious, perhaps, is that for generations gryptogamic botanists have been naming genera and species of lichens despite the fact that every lichen consists of a fungus and an alga. Some 15,900 of these "improprieties"—15,500 species and 400 genera—are now established in botanical literature. Surely they form ample precedent for paleobotanical species and genera of comparable biologic nature!

To the objection that similar stromatolites may have been produced by different assemblages of organisms, the answer is a question: Were they? And

if they were, are such examples of homeomorphy sufficiently common to cause confusion and to cast doubt upon the validity of form-genera and form-species for which no homeomorphs are known?

Among fossils whose biologic nature cannot be established, the most reliable indication of homeomorphy will be provided by form-species so widely separated in age that actual survival from most to least ancient cannot be reasonably assumed. If names alone were to be trusted, this test would be met by five Huronian and Beltian algal species which Maslov (1937) has identified in Paleozoic strata of eastern Siberia. His results are shown in this table:

Species	Age of Type Material	Age of Maslov's Material
Copperia tubiformis Walcott	Belt (Newland)	Upper Cambrian
Greysonia basaltica Walcott	Belt (Newland)	Upper Cambrian
Collenia undosa Walcott	Belt (Spokane)	Middle Cambrian
C. *compacta* Walcott	Belt (Siyeh)	{Middle Cambrian {Ordovician
C. *kona* Twenhofel	Lower Huronian	Ordovician

Doubt is at once cast upon this list by the appearance of *Copperia* and *Greysonia,* which are neither stromatolites nor organic. Maslov's supposed upper Cambrian examples, however, are slender laminated stromatolites which at least resemble undescribed middle or upper Cambrian forms from the Rockies of British Columbia. His *Collenia undosa* is an irregularly laminate form unlike anything in the Belt, while his *C. compacta* may be almost any stromatolite of the *Collenia* type. The supposed *C. kona* suggests a *Cryptozoon* related to *undulatum;* though the pieces figured are too small for recognition, they lack the highly convex laminae and large columns of Twenhofel's species.

In short, Maslov's supposed homeomorphs are mere examples of mistaken identity. Since other specific homeomorphs have not been described, the matter stands just where it did when Høeg wrote in 1929. It is a theoretical possibility, but one that has not materialized during fourteen years in which stromatolite genera and species have been multiplied. It therefore does not constitute a serious obstacle to the naming of such forms.[6]

As has been pointed out (Fenton and Fenton 1937, p. 1941; 1938, p. 2), recognition of genera and species among stromatolites rests primarily upon the stability of their characters. It is displayed by generally similar forms that do not intergrade, by forms that persist through thick formations despite sedimentary variations, and by those that have wide geographic range in clearly delimited horizons. *Cryptozoon* of the upper Cambrian (Ozarkian) and *Collenia* of the late Proterozoic provide the best-known examples.

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6 Even the undoubted existence of homeomorphs in formations of very different ages would not be much of a problem. Since it is inconceivable that a group of basically independent species should persist through several epochs or periods or should reconstitute itself after they have passed, such homeomorphs may be recognized as distinct form-species or form-genera. This will be analogous to the procedure by which biologists name similar geographic races that occupy widely separated ranges and had distinct origins, even though they came from a common ancestor.

We have seen that differences between modern algal deposits result from differences in organisms. Stability, on the other hand, implies that the algae responsible for each stromatolite species formed a persistent complex with its own group requirements and limits of tolerance. So long as these were met the complex survived, subject only to minor variations in response to external influences. But when environmental changes exceeded tolerance the complex was modified, reorganized or replaced by a wholly new one whose stromatolites may be distinguished as another species or even genus.[7] Thus each group seems to have had a distinct biologic basis, even though it was less clear-cut and specialized than the alga and fungus peculiar to each species of lichen.

Distinction must be made between minor variations and ecads. The former are not conspicuous and exhibit fluctuation; the latter are so distinct that they sometimes have been called separate species, and they are consistently related to recognizable environmental factors. They are comparable to the change from lithoid to dendritic tufa in Pyramid and Lahontan deposits, and they almost certainly represent modifications of the basic algal complex by loss or gain of species.

Where such modifications are discontinuous, it is both proper and practical to recognize the resulting stromatolites as species or subspecies. Thus *Cryptozoon minnesotense libertatis* (Winchell) seems to be the muddy-bottom, disturbed-water ecad of *C. minnesotense* Winchell (Fenton and Fenton 1939, p. 112). But where there is continuous gradation from one kind of deposit to another, as in *Collenia frequens* (Walcott) and some other Beltian form-species, such distinction becomes impractical. An alternative is to distinguish such ecads by adjectives, letters or numbers, on the assumption that they represent only temporary and partial changes in the basic algal complex.

A somewhat different situation is presented by variations in *Tetonophycus* and *Aulophycus* (Fenton and Fenton 1939), where ecologic relationships cannot be determined. The former resemble those in isolated dendritic tufa domes of Lake Lahontan (Fig. 11), also of doubtful significance. It seems best that both be designated as growth stages or phases, again upon the assumption that the organic changes which they reflect were not fundamental.

Stromatolites as Index Fossils

Since many stromatolites are stable in character and are widely distributed at definite horizons, they can be used as index fossils. At present their value is limited to deposits within individual basins of sedimentation; data justifying

[7] Replacements also were accomplished by migration, ecologic succession and evolution. Thus the appearance of *Cryptozoon ruedemanni* in place of *C. proliferum* within the Hoyt (Goldring 1938) seems to be the result of migration following at least local extinction, but the change from *Collenia frequens* to *C. versiformis* in a large biostrome of the Belt (Fenton and Fenton 1937, plate 17) indicates ecologic succession. The replacement of *Collenia* by *Cryptozoon* probably was brought about by evolution of algae that could grow in the distinctive pattern of the latter genus. These differences are significant, but they do not affect the general picture of stability.

more general use have not been assembled. Cloud (1942, pp. 368-369) thinks they will not be found, since "most stromatolites have no clear-cut characters from which one could say, for instance, that the beds in which they occur are Proterozoic or Silurian in age."

This conclusion seems premature, if not improbable. Cloud supports it by a list of stromatolites ranging in age from Huronian to Recent, all of which "would readily pass" for *Gymnosolen* Steinmann (1911) from the Ordovician(?) of Russia. The list includes some of the structures described by Maslov (1937), already discussed, and compares other forms whose resemblance is not obvious. There surely is no close similarity between the Eocene "reef" figured by Bradley (1929), Maslov's *Collenia umbellula* (1939) and Cloud's own drawing of *Gymnosolen*, after Pia, though his "digitate stromatolite of the gymnosolen type" (age unknown) does resemble the Archeozoic *Collenia septentrionalis* Fenton and Fenton (1939, p. 91). On the other hand, it is not at all difficult to distinguish *Cryptozoon* of the upper Cambrian (Ozarkian) from *Collenia* and other stromatolites of the Archeozoic, Proterozoic and lower to middle Cambrian.

It seems worth while, therefore, to seek additional information before deciding that stromatolites lack general value in correlation. To the writer, such information seems more likely to come from a careful check of form-species than from attention to genera, whose characters are none too well defined.

Conclusion

In conclusion, it seems well to rephrase a statement published some years ago (Fenton and Fenton 1938, p. 6). The most urgent need in study of stromatolites and other problematic algal structures is increased collections accompanied by elaborate field information. Many accounts of formations in which these problematica occur either do not mention them or do so in general terms, with no background of collections, notes and photographs for detailed study. Most museum specimens also lack such supplementary material, as well as descriptions and specimens of sediments from which the fossils were taken. Yet the very intimacy with which growth of algal complexes is related to conditions of the habitat demands a wealth of data that is not essential in dealing with fossils of more definite structure and form. Ancient stromatolites alone may mean little, but stromatolites supported by information on occurrence, growth relationships and enclosing sediments may be of great value in the understanding of these algal structures.

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A New Devonian Alga from Western Australia

Carroll Lane Fenton

In July 1940, Dr. Curt Teichert sent me several specimens of an unusual algal stromatolite found in dull red limestone of the "Upper Goniatite Beds" in Western Australia. Efforts to assign them to some previously described form were unsuccessful, and they therefore are made the basis of a new form-genus and species.

Stenophycus gen. nov.

Stenos, narrow; *phykos*, sea plant

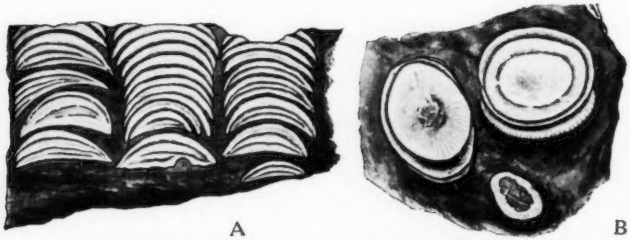
Small algal deposits forming closely spaced but distinct columns that are round to elliptical in transverse section. Superficially they resemble the much larger *Archaeozoon* Matthew of the Pre-Cambrian, but consist of more distinct layers and laminae. These are convex upward, with almost uniform curvature from center to margin; many are lenticular with pronounced central thickening. In most columns of which sections can be examined, the basal layer is flat beneath and convex above and rests directly upon the enclosing sediment.

Stenophycus teichertii sp. nov.

Description.—Essential characters of this species have been listed in the generic description. Specimens range from 3 to 8 mm. in diameter with heights exceeding 8 mm., since none is complete. Layers are 0.2 to 1 mm. in thickness, the thinnest consisting of a single lamina. The layers are irregularly arranged, so that their centers do not coincide; they also are separated by red sedimentary laminae 0.1 to 0.4 mm. in thickness. Layers apparently were loosely bound together in the columns. Both the holotype and a paratype show scattered layers in sediment below the principal algal band.

Occurrence.—"Upper Goniatite Beds" (=Oberdevonstufe III) of the Devonian. Types were found on a flat near the foot of an isolated hill about 2 miles west of Mt. Pierre, Kimberley Division, Western Australia.

Holotype.—Geological Museum of Princeton University. *Paratypes.*—Same institution and University of Western Australia, Crawley.



A B

Fig. 1. *Stenophycus teichertii* sp. nov., x3. A, vertical section through three columns, showing irregularity of layers and their separation. B, basal section at approximately right angles to the vertical axis, showing displacement of layers.

Monograph of the Paleozoic Cone Genus Bowmanites (Sphenophyllales)

J. H. Hoskins and A. T. Cross

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Introduction

Fructifications ascribed to the Sphenophyllales were known from compressions for many years before a cast of a specimen was first described by Binney in 1870. Fragments of petrified strobili with structure preserved were first studied by Williamson in 1871 (1876). As early as 1838 Presl described a specimen of Sphenophyllum under the name *Rotularia marsileaefolia* Sternberg which showed two laterally developed cones. Germar (1845) figured several species of Sphenophyllum bearing fructifications and in 1855 Geinitz illustrated a rather poorly preserved cone which he attributed to *Sphenophyllum emarginatum*.

A cast of a cone which has since been referred to Sphenophyllum (Zeiller, 1893) was found before 1840 (Binney, 1871) in a nodule of clay-ironstone near Pontypool, South Wales, by J. E. Bowman. Binney described this specimen as *Bowmanites cambrensis* in 1870 and published Bowman's original unpublished drawings (reprinted here, Figs. 27-31) in his memoir of 1871.

Since that time three* anatomically different types of cones, some associated with vegetative remains assigned to the Sphenophyllales, have been described under the generic names of Volkmannia, Bowmanites, Sphenophyllum, and Sphenophyllostachys. Only two of these three general types are known from material with structure preserved.

A petrified specimen representing Type I (Section *Simplices*) was first described by Williamson in 1871 (1876) under the name of *Volkmannia Dawsoni* from the Lower Coal-measures of England near Oldham. Later Williamson obtained and studied other specimens of the same type from calcareous nodules in the coal seams at Cinder Hills near Halifax, and from Dulesgate.

Another fragment of a cone of this same general type was recorded by Leclercq (1925) which she assigned to *Sphenophyllum Dawsoni beta*. The specimen occurred in a coal ball from the Bouxharmont beds of Werister. This horizon in Belgium is correlated with the Lower Coal-measures of England.

More recently (Koopmans, 1928) the Dutch Finefrau-Nebenbank horizon, which is also equivalent to the Lower Coal-measures, has yielded a preserved specimen which Koopmans has placed in this group. He suggests that it might belong to *Sphenophyllostachys Dawsoni* forma *alpha* or *beta* or even possibly *gamma*. This is more an indication of the confused status of the whole complex than a reflection on either his good work or the condition of the material.

Two other unnamed fragments of silicified sphenophyllaceous fructifications were discovered by M. B. Renault in the Grand 'Croix silicified magmas near Saint Étienne. He described and figured one of these in his early investigation upon the structure of Sphenophyllum (Renault, 1877) and later in his *Cours de Botanique Fossile* (1882). Zeiller (1893) studied and described the organization of the other as agreeing with *Sphenophyllum cuneifolium* and *S. Dawsoni*. The taxonomic position of these will be reviewed later.

The second general type of sphenophyllaceous fructification (Section *Jugati*), also known from petrifactions, was first found in the Middle Upper Carboniferous coal seam of Niedzielisko, near Jaworzno (Cracow), Poland and described by Solms-Laubach in 1895 as *Bowmanites Römeri*.

Another species of this same general type was first described as *Sphenophyllum fertile* by Scott in 1906 on the basis of a well preserved fructification from the Lower Coal-measures of Shore Littleborough, in Lancashire. Leclercq (1930) reported the discovery of some additional material of *S. fertile* from the Bouxharmont beds in the coal basin of Liege, Belgium which she later described in great detail (Leclercq, 1935, 1936A, 1936B, and 1937).

The third general group of sphenophyllaceous fructifications, Type III (Section *Conferti*), is not known from petrifactions. Hemingway, however, has recently (1931) made a careful study of some well-preserved compression

* A consideration of the natural affinities of Cheirostrobus referred by many authors to the Sphenophyllales lies outside the scope of this paper.

material. This group will be discussed in the taxonomic treatment of the genus.

The only other tangible record of a petrified sphenophyllaceous fructification of which we are aware, besides the specimen from Iowa herein described, appears questionable. Koopmans (1933, pl. II, fig. 21) figured a part of a section taken through a coal ball from the Aegir Horizon (basal Westphalian C or Lower Allegheny) in the province of Limburg (The Netherlands). This photograph which was made by reflected light from a polished and etched surface shows an oblique section through the tip of a strobilus which he believes to be a new species of Sphenophyllostachys. The maximum dimensions of this specimen by our direct measurements based on the photograph are three millimeters in diameter and five millimeters in length. No unquestioned sphenophyllaceous cone of such small dimensions has been recorded as far as we can ascertain. It is impossible to find in this illustration any trace of the elongated sporangiophores characteristic of all well known specimens. In view of the size, appearance, and arrangement of the sporangia and sporophylls it suggests the fertile tip of a branch of Cordäites (Cordäianthus).

The structure of a petrified strobilus found in 1941 (Hoskins and Cross, 1941, 1942) in a coal ball from the coal of the Des Moines Series of the Pennsylvanian Period in the Angus Mine, near Oskaloosa, Mahaska County, Iowa, enables us to modify the interpretation of certain morphological details. These findings together with the distinctive characters of this specimen warrant its description as a new species.

Because of the complex variations which appear in various modes of preservation, and because of the difficulties encountered in any attempt to establish diagnostic characters equally applicable to petrified material, compressions, impressions, and casts, it is not possible at this time to correlate the Iowa specimen with other known American material which to date has not been adequately studied. Fortunately some of the compression material from regions other than the United States has been more critically examined so that a comparison with available petrified material is possible. Such specimens are included in the following discussions.

The Structure and Affinities of a New Cone from Iowa

MATERIAL, PREPARATION AND PROCEDURE

The specimen of a cone in coal ball No. B-1706 from the Des Moines Series coal, Angus mine, near Oskaloosa, Iowa, was first exposed by a very oblique transverse section through the middle of the fragment. In the subsequent course of study nine additional cuts were made by the wire cutting technique which exposed in all, four true transverse sections rather regularly spaced, two radial longitudinal sections in the mid-portion of the cone, two obliquely transverse and two obliquely tangential sections. From two to thirty-five peel sections were taken serially from each surface. Each of the twenty surfaces is represented by a letter, i.e. 1706A-1706T inclusive. Representative peels from each series and, in several cases, the complete series of peel sections from a

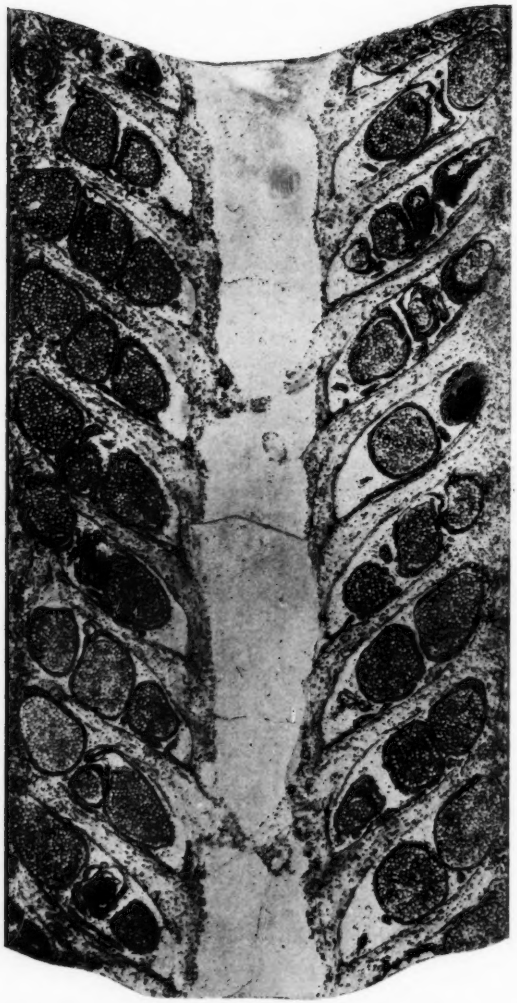

Fig. 1. Radial longitudinal section through the holotype specimen of the cone of *Bowmanites trisporangiatus* showing general features of the various organs. The vascular elements and the inner cortex of the axis have not been preserved. (Composition from B-1706 R2, 1706 R14, 1706 S2, 1706 S14).

single surface were mounted in Canada balsam. In all, of approximately 500 peel sections made, nearly 300 were mounted. Observations were made with various magnifications including the use of an oil immersion objective for the study of cell characteristics and spore sculpturing.

The preservation of the material is excellent throughout the mid-section (3 cm.) of the specimen. Neither the basal nor the apical ends of the cone were present at the time of fossilization and about one centimeter of each of the broken ends (abutting on the edges of the coal ball) is poorly preserved. One side is greatly flattened (Figs. 2, 3) indicating the position in which the cone lay as it fell into the plant litter. This flattening before fossilization indicates the fragile nature of the fertile shoots of the Sphenophyllales in general.

GENERAL MORPHOLOGY

The cone is not less than 1.6 centimeters in diameter at any point. There is no evidence of tapering at either end of the 6 centimeter fragment in our possession. Evidence shows that this specimen underwent some decay and disorganization before petrifaction. The decayed ends indicate that it was subjected to further deterioration after fossilization, i.e. during the chemical alteration (secondary pyritization) of the coal ball. The distal ends of nearly all the sporophylls are absent. Rarely can a fragment of the upturned portion be found (Figs. 1, 4, 5).

Each sporophyll bears upon its adaxial surface three elongated sporangiophores, each of which is terminated by a large, sub-globose sporangium. Some of the sporangia are displaced or entirely missing (Figs. 2, 3) on the unflattened side, and are quite crushed and distorted on the flattened side. Some free sporangia are found elsewhere in the same coalball and even some leaf-like fragments have been observed which may possibly be those of the missing sporophyll tips.

A radial longitudinal section through the axis parallel to the bedding plane, or flattened side, gives the true appearance of the structure of the cone (Fig. 1). Similar sections taken perpendicular to the bedding plane show excellent organization on one (upper) side only, with an almost unrecognizable tangle of crushed sporophylls, sporangiophores and sporangia on the other (flattened) side.

AXIS

The average diameter of the axis based on direct measurement of the four widely separated transverse sections is 4.5 mm. The greatest diameter of about 6 mm. occurs at the nodes. Such a nodal swelling is typical for most of the Articulatales.

The entire stele of the axis is missing as is the surrounding zone of inner cortex, which, in other species, is made up of several layers of very delicate parenchyma cells. The nature of the stele, i.e., whether triarch or hexarch in arrangement of the xylem, is thus unknown. This important structure must be sought for in the recovery of additional material.

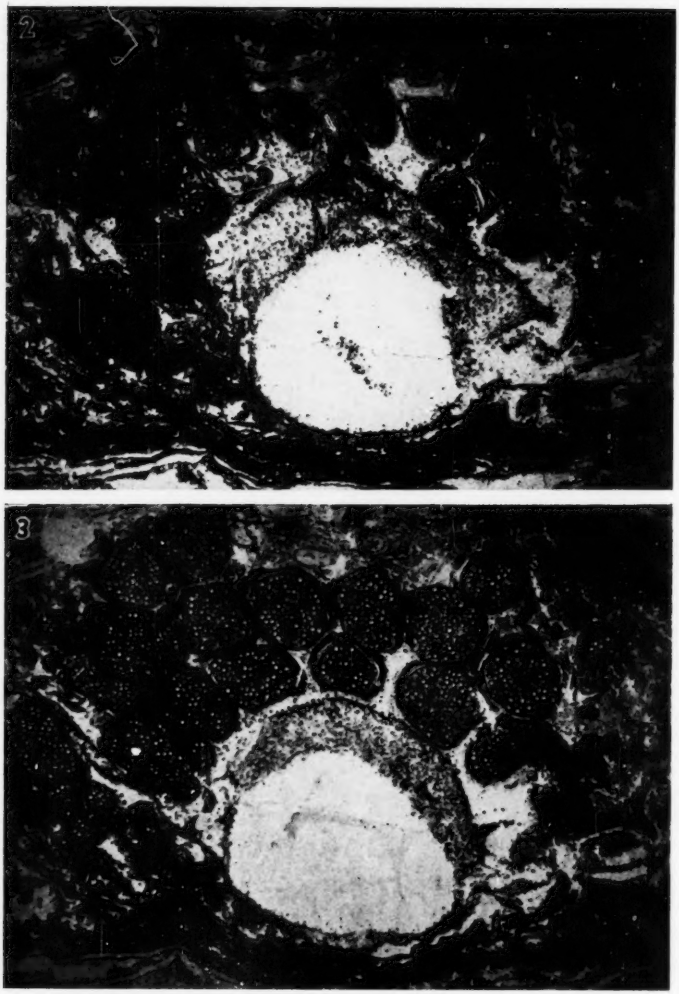

Fig. 2. True transverse section of the cone of *Bowmanites trisporangiatus* through the region of a node. (Compare with Fig. 3). The increase in thickness of cortical tissue and the decrease in the number of sporangia at the node is typical. (1706 N1)

Fig. 3. Transverse section taken through an internodal region, somewhat lower than the section shown in Fig. 2. Note that the sporangia occur in three concentric verticels and in radially arranged rows from the axis. These rows indicate individual bracts. Microscopic examination of serial sections of the crushed side show it to have about 9 radial rows making a total of 18 bracts and rows of sporangia. (1706 N9)

The outer cortex of the axis is fairly well preserved. It is composed of rather firm-walled, well-organized parenchyma cells which are sharply reduced in size toward the periphery of the axis. The course and disposition of the sporophyll traces through the outer cortex are clear. These bundles traverse the outer zone in an upward and outward direction in approximately one-third the length of an internode (Figs. 5, 7, 8). There appears to be a serial sequence of bifurcations resulting in the single vascular bundle of each individual sporangiophore and bract. The problem of the true nature of these bifurcations (Hirmer, 1932B, 1933, Troll, 1933) cannot be reviewed here but will be dealt with in a later paper.

The internodes are about 1.5-2.0 mm. in length and the greatly thickened bract bases occupy about one-half this distance (Figs. 1, 4, 5).

Several foreign rootlets traverse the hollow central area of the axis (Figs. 1, 2).

SPOROPHYLLS

The fertile leaves or leaf-like organs which bear the sporangia in sphenophyllaceous plants are the so-called sporophylls or bracts. These appendages appear to bear the sporangiophores and sporangia superficially on their upper (morphologically ventral or adaxial) surface. The two principal interpretations, the Bower theory and the Scott-Hirmer theory of the origin and phylogeny of the sporangiophores and sporangia and the sporophylls are sharply contrasted. The former theory would derive the sporangiophores with their sporangia earlier and independently of the sporophylls. Scott, Hirmer and others consider these structures to be of common origin and subsequently divided. They have not reached an accord on the interpretation of the nature of the division of these appendages. These problems cannot be investigated here. Works by Benson, 1908; Bower, 1903, 1908, 1911, 1935; Browne, 1908, 1909, 1927; Coulter, Barnes and Cowles, 1910; Hickling, 1907, 1910; Hirmer, 1927, 1932A, 1932B, 1933; Lignier, 1903; Lotsy, 1909; Schoute, 1938; Scott, 1920, 1923; Seward, 1898, 1910; Sykes, 1908A, 1908B; Tansley, 1907; Troll, 1933; Walton, 1940; Williamson, 1876, 1890, 1891; Williamson and Scott, 1895; Worsdell, 1905 and Zieller, 1893, consider various phases of this controversy in considerable detail. Our material is inadequate to furnish conclusive evidence to substantiate any of the present interpretations.

We will first consider the lower portion which is usually referred to independently as the sporophyll. The sporophyll is a leaf-like structure comprised of a relatively horizonal portion, the pedicel, which diverges from the axis at a remarkably uniform angle of about 60°, and a more or less erect distal portion, the lamina. In this species as in most, the point of juncture of these two parts is indiscernible and the lamina curves evenly upward from the pedicel and overlaps the lamina of the superior sporophyll. The overlapping of the laminae may be definitely imbricate if these free tips of the sporophylls rise more or less vertically from the pedicel, but in many cases the sporophylls are only aristate and divergent, whereas in a few forms they do not overlap at all

Fig. 4. Radial section of cone showing attachment of sporangiophore to sporangia. A sporangia of the third node is shown as it becomes free from the bract in "third position."

(*Bowmanites fertilis, B. trichomatosus,* etc.). Occasionally the distal portion of the pedicel is subtended into a heel or spur as in *B. angustifolius* (Fig. 18).

The sporophylls of our specimens are arranged in superposed whorls upon the axis. It appears that this is a sound generic character. Occasional reports of alternating whorls have been made (Zeiller, 1893, Williamson and Scott, 1895), but distortion during compression may be held responsible in the case of *Bowmanites cuneifolium* and reinterpretation of Williamson's specimens may be in order. The definite superposition of consecutive whorls of sterile Sphenophyllum leaves justifies the expectation of a similar condition in fructifications of the order. Also those species which do not produce true cones (*B. charaeformis, B. major,* etc.) seem to have definite superposition of whorls of fertile leaves.

The number of sporophylls per whorl is difficult to determine because of their lateral confluence into a collar or disc surrounding the axis, but 18 were counted in four different sections. This number may be more readily determined by a study of oblique tangential sections such as that shown in Fig. 10, where the vascular bundles of the sporophylls are evident, and the free tips of the bracts are exposed as transverse sections. There is always one vascular bundle per bract. The number 18 may have no significance, for the number of bracts per whorl seems to vary from 14-20 in undoubted specimens of *B. Dawsoni.* Transverse sections (Figs. 2, 3) show 18 radial rows of sporangia above the whorl of bracts which is also indicative of the number of bracts, as will be pointed out in the discussion of the sporangia. The pedicels are laterally coalescent through about one-third of their length, i.e., for about 2 mm.

The principal body of tissue of the pedicel is a strong parenchyma continuous with and scarcely distinguishable from that of the outer cortex of the axis. Toward the distal end and in the more fragile laminal portion of the bract this parenchyma more nearly approximates the delicate tissue of the inner cortex of the axis. The thickness of the pedicel diminishes, accompanied by a decrease in number of cells from the point of attachment to the axis, where it is about 1 mm. thick, to about 0.5 mm. in thickness distally. One or two rows of smaller cells are immediately subjacent to the clearly differentiated epidermis.

A slender vascular bundle traverses the middle of the bract just below its upper surface. It is composed of but few xylem elements, the smaller spiral members being exterior to the distinctly larger scalariform tracheids. This corroborates the statement by Williamson and Scott (1895, p. 936) that the xylem of the leaf trace bundle is centripetal. It is not possible to identify the phloem.

SPORANGIOPHORES

The sporangiophore is a long (2.5-6.0 mm.), slender, stalk-like structure, about 0.1 mm. in diam. for most of its length. Usually the distal end (0.3-0.5 mm.) is gradually enlarged until it is about 0.4 mm. in diam. where it fuses indistinguishably with its sporangium. The sprorangiophores are three times as numerous as the sporophylls, i.e., there are three sporangiophores per bract. They arise separately, side-by-side on the bract surface and close to the

Fig. 5. Radial section showing "third position" sporangiophore arising from the lowest bract (sporophyll), and "second position" on the middle and upper bracts. The fragment of the sporangiophore above the stub of the sporangiophore arising on the middle bract belongs to it as is shown by serial sections. The outermost sporangium of the lowest bract has been cut quite obliquely and shows the peculiar nature of its epidermal cells. Dark areas below the point of juncture of the bract with the axis are vascular traces. (1706 R2)

axis (Fig. 10). In a tangential section through the cone near the axis, they first appear as mounds of tissue, slightly, yet distinctly delimited from the surface of the bract (Fig. 10). In a radial section of the cone, they appear as densely organized, radially elongated, ridges of special tissue which become separated from the bract surface within 0.3 mm. from the axis. This separation occurs in three distinct positions, i.e., (1), axillary, (2), between 0.1-0.15 mm., and (3), 0.15-0.25 mm. for the three laterally adjacent sporangiophores of each bract. We have not been able to ascertain whether the sporangiophore which bears the innermost sporangium always arises in the same position, i.e., between the other two or on the right or left side of the bract base, etc. Neither have we been able to prove that the sporangiophore which first becomes free from the bract surface (Fig. 7) bears the first sporangium; that the sporangiophore arising in "second position" (Fig. 5) always bears the second sporangium, and that from "third position" (Fig. 4, 5, 8) the outermost sporangium, but in several cases this is known to be true. We have found no cases to the contrary.

Due to the flexible nature of the sporangiophore and to the crowded conditions of the sporangia, the sporangiophores follow a tortuous course to their terminations and may therefore be traced only by observation of serial sections. Various accessory hooks and loops occur (Fig. 4). For instance above the third bract on the righthand side in Fig. 1, the single sporangiophore has been cut through, transversely, four times (serial sections make possible the confirmation of their continuity).

The course of the mature sporangiophores generally extends along the upper surface of the pedicel to a point beyond their respective sporangia, where they rise vertically almost to the lower side of the superior whorl of sporophylls, then become noticeably inflated or expanded and sharply recurved toward the axis (Figs. 1, 9). The epidermis, which is strongly differentiated throughout, becomes even more accentuated by an unusual increase in size of the cells and thickness of their walls in the terminal portion of the sporangiophore. These cells also seem to contain considerable organic residue.

In transverse section, the sporangiophores are usually rounded (Fig. 14) but occasional heart-shaped or even invaginated sections are found. The epidermis, which is occasionally more than one cell thick at the distal end of the sporangiophore, surrounds a weak hypodermal tissue. Between this and the vascular bundle there is a space marking the former presence of delicate parenchyma. The vascular bundle is apparently collateral and consists of several xylem elements. The number of tracheids increases distally through the course of the sporangiophore until as many as 20 are present at the distal extremity. Most of the tracheids are spirally thickened, but occasionally scalariform tracheids are found.

In a series of sections taken from surface 1706A and others of our specimen, we have evidence that the vascular strand approaches the node vertically and outwardly and forks dichotomously at a point about 0.5 mm. from the angle formed by the attachment of the sporophyll with the axis. One strand passes

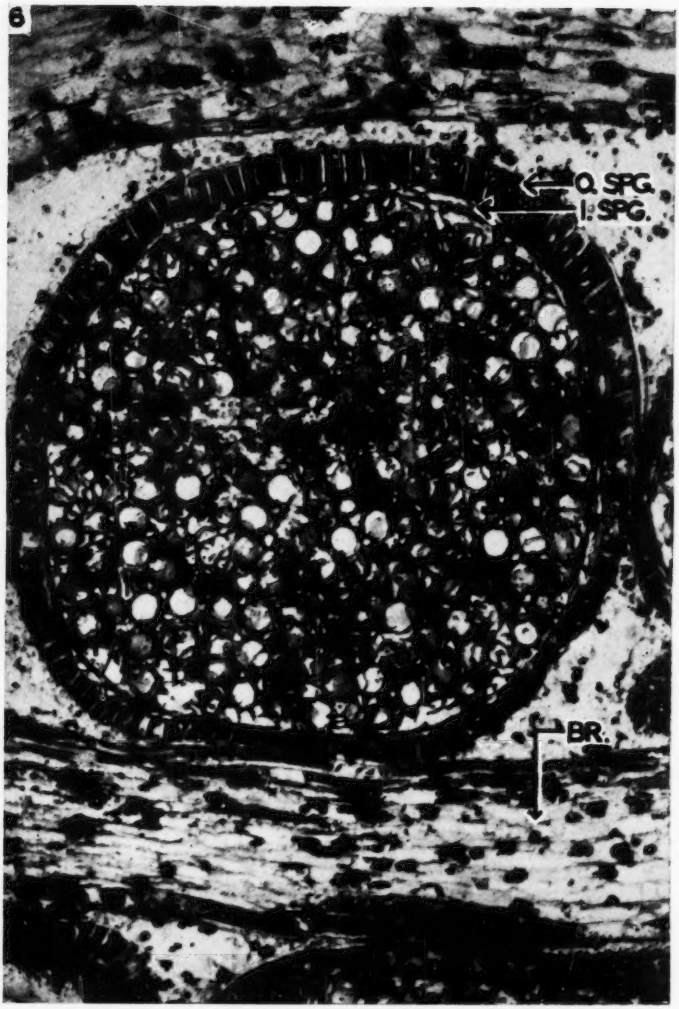

Fig. 6. Single sporangium shown in true median section. Note that it rests on the bract (BR) below and almost touches the one above. The crushed, delicate inner sporangial wall (I. SPG.) is clearly visible. The general, gradual decrease in the size of the much-thickened cells of the outer sporangial wall (O. SPG.) from the upper distal side to the lower and axial side is quite evident. (1706 R14)

from the cortex into the sporophyll and does not divide further. The other strand divides immediately, one of the resulting bundles supplying the sporangiophore in "Number 3" position, while the second bundle undergoes a further bifurcation. The resulting two bundles pass outward through the cortex to the base of the sporangiophores at slightly different levels, the lower one supplying the sporangiophore in position "Number 2" and the upper one the sporangiophore in position "Number 1." It must be remembered however, that all three traces supplying the sporangiophores emerge from the axis in the same transverse plane. The sections 1706A 3 to 7 show this series completely. We have no reason to believe that this is not the normal condition.

SPORANGIA

Three sporangia are borne linearly above each sporophyll member of the whorl. They are not less than 1.5 mm. in shortest diameter and some are at least 2.4 mm. The sporangia are borne at the enlarged tips of the sporangiophores which bear the same relationship to them as the funiculus does to an anatropous ovule (Figs. 4, 9). The sporangium rests directly on the surface of the sporophyll below and reaches the base of the sporophyll above. This condition shows clearly in true median section (Fig. 6) and in oblique tangential section (Fig. 10). The sporangiophore passes to one side or the other, never immediately beneath the sporangium. It sometimes causes a slight furrow (Fig. 10) on the lower side of the sporangium. Distally it attaches to one side or the other of the top but never directly in the middle. The sporangia are crowded closely together and very rarely (Fig. 3) one of the sporangia in the inner of the three concentric verticels does not develop. In such a case, there are but two sporangia per individual sporophyll. This spatial relationship results in a dense, crowded cycle of sporangia nearest the axis. The second and third verticels are successively less crowded. (Compare Figs. 1 and 2 with Fig. 10).

There is no justification, according to the general picture given by our material, for such an hypothetical areal distribution of sporangia as proposed by Hirmer (1927, Figs. 417, 419, 421). Nor do the illustrations by Binney (1871), Williamson (1874, 1876, 1890), Williamson and Scott (1895), Solms-Laubach (1896), Leclercq (1925), Koopmans (1928), and others, support this proposal. Rather they indicate, as does our material, that the diameter of the sporangia is not less than the width of the sporophyll and normally fills the space between successive whorls of sporophylls. Thus from a space relationship alone the arrangement suggested by Hirmer appears impossible. There is, moreover, no evidence of collateral pairing of sporangia on any sporophyll with the possible exception of those of *B. fertilis* and *B. Römeri*. Rather the sporangia occur quite uniformly linearly arranged above each sporophyll.

The sporangial wall is made up of two principal layers. The outer, or epidermis, is comprised of a single layer of greatly thickened cells. They are as large as, and continuous with the epidermal cells of the distal end of the sporangiophore, and are indistinguishable from them. There appears to be a

Fig. 7. Enlarged section showing attachment of bract to axis of the strobilus. The vascular bundle supplying the sporangiophore of "first position" (axillary) is not shown. The vascular bundle which seems to lead to it is shown in other sections to supply a sporangiophore which arises from that bract surface in "third position." Note the point of bifurcation of the bundle, one half of which supplies the sporophyll. (1706 R16).

gradual diminution in size of the cells of the sporangium in all directions from this point of attachment (Fig. 6). When the sporangia are densely crowded as in the first vertical (adjacent to the axis) their lateral walls are often quite thin. This may be attributed to lack of development due to pressure. The thickening is occasionally irregular and gives the superficial appearance, in some cases, of an annulus. Though such a structure has been suggested (Zeiller, 1893; Williamson and Scott, 1895), and may be within the realm of possibility, serial sections fail to support the idea. The method of dehiscence is unknown. The occasional stomium-like organization of the sporangial wall as seen in transverse section apparently is nothing more than the result of the proximal position of the sporangiophore as it circumscribes the distal side of the sporangium.

The inner sporangial wall is made up of 2-4 layers of very weak, thin-walled, parenchyma cells which are usually collapsed. These are much smaller than the epidermal cells (Figs. 4, 6, 7, 9a, 9b, 14) and are apparently continuous with and indistinguishable from the delicate inner tissue of the sporangiophore (Figs. 4, 9a, 9b). The vascular bundle of the latter organ is terminated abruptly just before reaching the inner margin of the fragile hypodermal tissue. The termination of the vascular bundle is probably the only distinguishing point which marks the end of the sporangiophore.

The sporangia are densely packed with conspicuous spores which will be discussed in the following paragraphs.

SPORES

The spores appear to be uniform and though there is some variation in size, there is no evidence of heterospory in our specimen. Spores in the same sporangium range in size from about 75 μ to 125 μ exclusive of the ridges and "spines," shown in Fig. 11. These ridges usually do not exceed 25 μ and the overall diameter is thus about 100-150 μ. The case of heterospory reported by Renault (1877) was based on an erroneous observation, i.e., a peculiar tangential section through a sporangium (Fig. 17b) was mistaken for a section through a megaspore. Zobel's report of heterospory (1910) has also been generally disproved. It is conceivable that some of the spore mother cells or even some of the individual members of the tetrad developed less completely than others, or were even completely abortive in a sporangium so tightly packed with spores. This and imperfect sections also account for Thoday's misinterpretation (1906).

Spores of sphenophyllaceous fructifications have been figured by several authors. The highly characteristic ornamentation of the spore wall has been more or less confused. Williamson and Scott (1895, p. 939) state that "their cell-wall possesses a highly characteristic ornamentation, consisting of prominent spines, which are connected together on the external surface of the exosporium, by a reticulum of elevated ridges." Knox (1938A, Fig. 120) shows a single spore taken from *Bowmanites Dawsoni* as having much enlarged, prominent spines, connected by lesser ridges. This is not the case according to

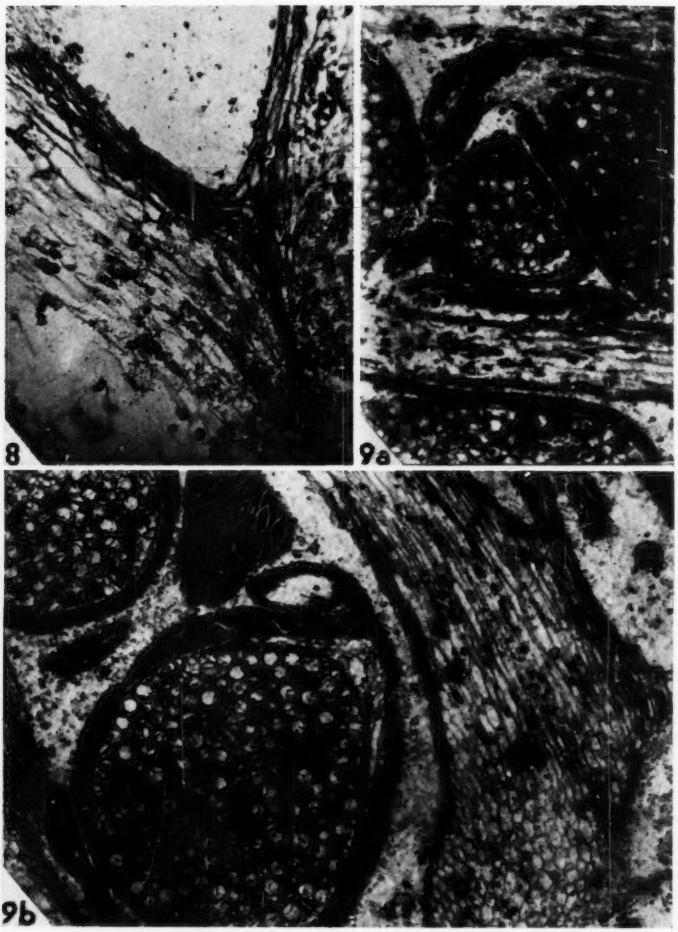

Fig. 8. The sporangiophore which is given off the bract (left) in "third position" is shown here to be supplied by a vascular bundle which is the adaxial (inner) segment of the division of the leaf trace (lower right).

Fig. 9a. Enlarged sporangium showing increase in size of the sporangiophore as it rises from its subtending sporophyll and extends to the base of the bract above and there bears the sporangium in an anatropous fashion. In this section, the sporangium appears pyriform. This is due to the attachment of the sporangiophore to one side or the other of the sporangium rather than directly in the middle of the distal side.

our material, from which pictures have been obtained (Figs. 12, 13) which are almost identical with those shown by Williamson (1890, Figs. 17, 18) and some of those figured by Knox (1938A). Rather maceration of the sporangia and isolation of the spores show a continuous network of heavy ridges with a somewhat bipolar orientation. The large "false spines" which are well shown in Fig. 12, a photograph made from a thin section, appear to be remnants of an additional cell membrane. These prominences or bits of tissue are lost in ordinary maceration, but careful reduction of the sporangial matrix by dilute acid does not destroy this rather delicate tissue. Spores isolated by the latter method and observed when floating freely in a medium of glycerin-alcohol or glycerin jelly show this ridged membrane to be continuous over the entire surface of the spores, even to the extent of covering, occasionally, the tetrad scar of the normal exine beneath. The true exine has a pustulose or granular external surface broken only by the prominent triradiate tetrad scar which extends only about one-third of the way to the margin of the spore (Figs. 11, 13). This spore wall is clearly visible in most specimens subjected to normal maceration techniques. A definite intine or endosporium is not easily demonstrated.

Spores with multi-layered exines are not uncommon. Those which show this condition, normally retain their multiple walls when subjected to strong acids. Apparently the spores of the sphenophylls are covered not only by an exine which may or may not be multi-layered but an additional coat similar to the episporium of various fungi and algae and the perisporium of some of the Equisetales and Filicales of the Pteridophyta. We might expect such a structure to be present. Living members of the Equisetales have a definite additional spore membrane surrounding the exine which splits into characteristic ribbons commonly referred to as "elaters." Beer (1909) has shown that there are four distinct layers in the walls of Equisetum spores. Two of these layers, the exosporium (exine) and the endosporium (intine), are derived as secretions of the spore protoplast in the order listed. The other two layers, the "middle layer" and the elater membrane (perisporium), are products of the activity of the disorganized tapetal cell protoplasts, the so-called periplasmodium. Hannig (1911A) supports this theory of development and organization of the spore wall in Equisetum and applies it also, with modifications, to the more specialized spores of Azolla, and to various groups of the Filicales. In a later paper (Hannig 1911B) he attributes even greater importance to the perisporium and

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Fig. 9b. Another section of a sporangium showing attachment of sporangiophore. The vascular bundle of the sporangiophore may be seen on the side nearer to the sporangium. The inner tissue of the sporangiophore, which is continuous with that of the inner wall of the sporangium, is shown rather clearly. Note also in this section the unusual character of the outer wall of the sporangium which appears to be two cells thick near the point of attachment. This apparent condition is due to the nature of the section. A sporangiophore is given off the upper surface of the superior bract (to the right) in "third position." The forking of the vascular bundle is also shown.

Fig. 10. Enlargement of a portion of a section similar to that shown in Fig. 15, i.e., a slightly oblique transverse section through the strobilus. The axis (AX) is to the left of the picture. Portions of two successive whorls of bracts (BR) are shown. The bracts shown to the left are fused into a collar and at the bottom of the picture the sporangiophores appear as humps on the upper surface of these sporophylls (to the left), whereas they appear as free organs higher up because of the greater distance from the axis. The bracts shown at the right are sectioned just at the point where they begin to separate

emphasizes the possible taxonomic value of its presence or absence on the spores of various ferns. Bower (1923) further exploits this idea and believes that it has greater significance as a taxonomic character than the sculpturing of the exine. It is absent in the Eusporangiate and the more primitive Leptosporangiate ferns, but generally present in the more advanced members of the Leptosporangiates.

In the ferns the perisporium appears to be a membrane (thin at first and later quite thick) loosely surrounding the exospore and showing a varying number of folds and ridges. The constancy of the resultant configuration is not definitely known. Hannig believes that the perisporium is derived from the surface layer or membrane ("Hautschicht") of the vacuole in the periplasmodium in which the spore is contained.

It is conceivable that another class of the Pteridophyta, the Sphenophyllales, possesses a similar structure either in some or in all of its members. In our material this layer, the perisporium, is present and clearly distinguishable. Many previous figures of recognized sphenophyllaceous spores illustrate a similar structure. Paget (1936), in an attempt to correlate with their natural groups the spore types which Raistrick and Simpson (1933) arbitrarily designated by letters and numbers, came to the conclusion that all spores assigned to Group E belonged to the Sphenophyllales. But Knox (1938A) considers this assignment as wholly inconsistent with the knowledge of spores definitely identified (by evidence of organic attachment). Her skepticism is justifiable to some extent, although our findings show that Paget's suggestion is not unfounded. Nearly all spores of Group E figured by Knox are readily referable to the Sphenophyllales when we consider the known range of variation and the fact that the perisporium may occasionally be absent because of lack of development, failure of preservation or destruction by maceration. Figures based on studies of thin sections are the only ones of those heretofore made, which can be reliably accepted. Isolated spores must of necessity be correlated, not with a typical example, but with generalized figures showing the range of variation. We believe that the perisporium is not equally well developed on all spores of a species or even among those of the same individual or sporangium. Fig. 13 shows distinctly the possible variation in adjacent spores of a single sporangium.

The spores figured by Carpentier (1932, pl. XV, figs. 1-5) probably do not belong to Sphenophyllum as he has indicated but to a very unusual and interesting new form. Spores illustrated by Scott (1897) for Cheirostrobus apparently lack a perisporium though they do resemble closely Bowmanites spores after the removal of the perisporium. This condition might be of value as a distinction between that genus and Bowmanites, though the available evidence of the presence of the perisporium in all species of Bowmanites is still incomplete.

(BR. S.) into individual bracts. Note the two sporangiophores just above the bract surface (to the left). There are only two sporangiophores per bract, one at either side of each sporangium, at this distance from the axis. The lateral distortion of the sporangia due to crowding and their typical arrangement in one plane are clearly shown.

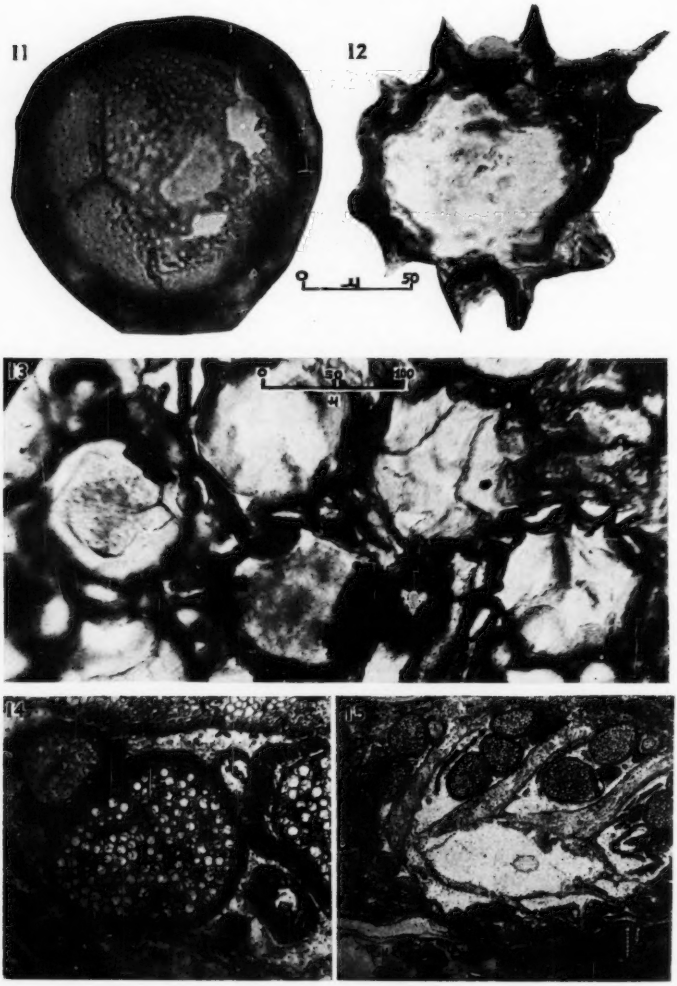

Fig. 11. Enlarged spore showing pustulose wall, the exine (exosporium), with definite tetrad scar.

Fig. 12. Spore showing "spinose" appearance of ridged perisporium.

Fig. 13. Habit showing variation of spores in one small area. The spore to the left is very similar to that shown in Fig. 11 and the spore to the lower right corresponds to Fig. 12.

AFFINITIES

Apparently all these characters clearly differentiate our specimen from known fructifications and it is therefore designated as a new species.

In our attempt to name, classify and correlate it with other sphenophyllaceous fructifications we encountered numerous serious discrepancies and conflicts in previous reports. Further we were unable to discover any consistent use of distinctive characteristics in previous descriptions of new species. In order to assign our specimens definitely, it was necessary to investigate all previous reports of fertile shoots of the Sphenophyllales and to show by comparison the obvious discrepancies and points of confusion. The following discussion gives the pertinent information and provides the basis for the revision of the entire genus. In the taxonomic treatment as complete and uniform a description as possible is given of all known species, together with that of the new species from Iowa.

Bowmanites as a Valid Organ Genus

The taxonomic problems of the paleobotanist are different from those of the student of modern floras. The paleobotanist must base his studies on such parts or fragments of plants as may come to hand. After proper study and comparison, and in the absence of complete or accurate reconstructions, it is often necessary to arrange these fossils in organ genera, within which species may well be recognized.

As we are considering the taxonomic relationships of such an organ genus of fossil plants composed in part of detached cones, we are obliged, in conformance with proper taxonomic usage, to select for these isolated specimens the oldest usable generic name. For reasons shown in the discussion of the history of the genus following this introduction, we must accept the name Bowmanites Binney (1871) for the organ genus based on isolated cones generally referable to the stem and leaf organ genus Sphenophyllum.

But the taxonomic problem is actually even more complex. This case is not the only difficult one, for the study of many other groups of fossil plants including the well-known genera Lepidodendron, Sigillaria, Calamites, Annularia, etc., is equally impeded by problems like the following. Certain attached cones which obviously belong to the same genus and even species as certain detached cones, as based on adequate morphological criteria, are also known under different names, i.e., the names applied to the vegetative organs to which they are attached. Further the two organs may be included in a third name which has been applied to the natural genus and species to which both belong,

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Fig. 14. Section showing difference in size of sporangiophores, depending on the proximity to the point of attachment to the sporangia. The structure at the lower right of this figure is a tangential section through a sporangium.

Fig. 15. Oblique longitudinal section showing fusion of bracts into a collar at left. Note the deformity of the bract bases on the crushed side. Parts of three whorls of bracts are shown.

although they also belong to distinct organ genera. The last name may be applied only after the relationship between the organs of the complete plant has been proven. But until then, what generic reference is to be made to all cones belonging to the same genus whether attached or isolated in occurrence?

We cannot within reason agree to the use of one name for the form genus of certain species of detached cones and another name for additional specimens of the same species if they are attached to a leafy branch! Any plant as a natural organic entity should have but one name. But when certain plant fragments are only doubtfully related to other organs of a similar plant, do we want to lose or discard these doubtful fragments by not naming and recording them or do we want to keep them in the literature and before the paleobotanists by applying to them a workable, usable name? If this is done, pending eventual unquestionable correlation, these specimens may ultimately be included in the description of the whole plant.

Organic connection is the only undoubted means of correlating definitively two fragments of plant remains found preserved in the rocks. It is possible that such a correlation may then be followed by assigning numerous other known but detached specimens of plant fragments to their proper entity. Dependable and constant characteristics must be selected which will always hold good in correlating isolated remains. These distinct characters must be present in the original specimen which shows the organic connection of the two organs. Furthermore, careful study must establish, tentatively at least, the nature of both of the plant organs and the possible range of variation which each shows or may show either alone or in relation to the other. By comparison, the value of additional distinctions based on characteristics found only in isolated specimens of either organ is questionable.

Paleobotanists cannot base their identification of additional specimens showing organic attachment solely on the distinctive criteria of either organ. They must establish the identity of both organs, even though connected, by the correlation of each with the original criteria. Cases of leaf dimorphism must be expected, and the natural range of variation of the leaves of the same species and even of the same specimen often exceeds the differences which are considered to be of specific value. Conversely, the leaves of several species may be indistinguishable, and specific determination must then be based on other organs or combinations of organs. Cones may be expected to vary considerably in size and even external appearance, depending on maturity, conditions of growth, etc. Students of compression or impression materials often identify their genera and species solely by characteristics of the vegetative remains and not by means of attached fructifications. Consequently in many cases, of which *Sphenophyllum cuneifolium* (Sternberg) Zeiller is a good example, leafy branches are identified by certain vegetative characteristics and cones attached to these branches have rarely been studied in detail. On the basis of indirect evidence the attached cones are in this case considered to be identical with the petrifactions known as *Sphenophyllum Dawsoni* Williamson which are found with

some frequency in the English Coal-measures and less commonly elsewhere. Our studies show that *Sphenophyllum Dawsoni,* as generally known, is not a single species but a complex of at least three, so far heretofore distinguished only as forms. Consequently the foliage of Sphenophyllum alone is at present inadequate for true specific determination, at least as far as the basic distinguishing criteria are concerned which are used to separate the leaf species. Several similar cases might be cited. This is not an unusual situation even for the student of modern plants. It is obviously impossible to differentiate clearly between the numerous species of Quercus, Chenopodium, Carex, Panicum, etc., on the basis of leaf characters alone, or at least on the basis of the external characters now used. Galium, a genus of small herbaceous seed plants (Rubiaceae), somewhat resembles the ancient Sphenophyllum in habit and general appearance of the arrangement of the whorls of leaves on the angular stem. It is difficult, if not impossible, to distinguish correctly many of the recognized species of Galium on the basis of external characters of the leaf alone. Reproductive organs would provide a more accurate method of identification than leaves. Such organs as cones, flowers or seeds are less variable within the limits of a species and provide more adequate criteria for specific distinction. Certainly a combination of both leaf and cone characters would furnish still more reliable criteria.

It is within the realm of possibility that more diagnostic leaf characters could be utilized with greater accuracy. Anatomical characteristics of leaves appear in some respects to be of more specific value than external characters. However, tissue arrangements, stomatal and cuticular structure and other similar features must be used with caution and require a good knowledge of the possible ecological variations.

We believe that many of the identifications of other organs of sphenophyllaceous plants are incorrect or inadequate. Most of these errors are due to lack of sound criteria. A re-working of all species now grouped under the generic name Sphenophyllum would undoubtedly reveal many broad discrepancies and such large species as *S. majus, S. cuneifolium, S. emarginatum,* etc., would be recognized as polymorphic, i.e., groups containing several distinct species, not strictly divisable by superficial leaf characters. Some species might be combined with others after the discovery that leaf dimorphism is present.

Recognizing the discrepancies and ambiguities involved, we are, in the interest of clarity and good taxonomic usage, obliged to refer to the genus Bowmanites not only those cones which are known merely as fragments isolated from vegetative parts but also all other undoubted species and specimens of the same genus, whether directly connected or only indirectly associated with vegetative remains.

History of the Genus Bowmanites

In the attempt to classify our specimen as a species of the fructifications of the Sphenophyllales we encountered great difficulties because of the present

confused status of the classification of these fossils. To begin with, the name Sphenophyllostachys as applied to the cones referable to the genus Sphenophyllum, only recently gained favor among leading paleobotanists (Hirmer, Zimmerman, Walton). This name, though recognized at its inception by Seward (1898) as a sesquipedalian one, would normally be acceptable because of its meaning, i.e., designating the cones or strobili of the Sphenophyllales. Unfortunately, for reasons of priority, the validity of the name is questionable.

According to the present rules of botanical nomenclature, and more especially those pertaining to paleobotany, we are obliged to use the first name applied to a plant or group of plants since 1820, the date selected for absolute priority of fossils, as long as this name has been validly published, unless strong evidence is submitted that any change of a name well established by long and consistent usage would create serious confusion. In such a case steps could be taken to have that name retained as a *nomen conservandum*.

For reasons well known to all who work with the fragmentary remains of fossil plants, it is necessary to set forth generic designations for various plant organs as well as for entire plants. Obviously this necessity poses additional taxonomic complications but in reality is a convenient simplification of the task of assigning organs or fragments of organs to the plants which bore them. Organic connection is the only proof of definite relationship, but evidence of an organic connection between two plant fragments in one case may not be regarded as proof of the fact that all similar specimens must bear identical relationship. One reason for this awkward situation is the necessity of considering the time relationship in addition to the geographic and structural relationships. However, we do not doubt that the cones considered in this paper represent a well known, important and distinct Paleozoic cone genus belonging to the Sphenophyllales, and generally referable to the vegetative remains known as Sphenophyllum.

In his excellent memoir (1893) Zeiller claimed that certain previously described fructifications were undoubtedly those of Sphenophyllum and that the *Bowmanites Dawsoni* Williamson cones as well as certain others, except two (Renault's silicified specimens from the Grand 'Croix near Saint Étienne) known only from impression material, were, with some leaf remains, referable to *Sphenophyllum cuneifolium*. This interpretation was generally considered sound and was subsequently adopted in principle by various authors (Williamson and Scott, 1895; Seward, 1898; Kidston, 1901; Scott, 1906, et al.). The statement that all similar attached or isolated specimens from horizons widely separated geologically and geographically are similarly related is untenable. Recognizing this difficulty, Seward (1898) proposed the distinct organ genus Sphenophyllostachys for the cones assignable morphologically and/or anatomically to the genus Sphenophyllum, but whose organic relations with the plants could not be shown. However, at least two other generic names had been created earlier than Seward's for cones now known to have sphenophyllaceous affinities.

Volkmannia Sternberg (1825), one of these early cone genera, included elongated, distichous cones arranged either on lateral branches or at the tips of stems. Most of the diverse specimens included in this heterogeneous group were correlated with vegetative remains of Asterophyllites, others with Calamites and a few with the Sphenophyllales. The first species described, *V. distachya* Sternberg (1825), was later (1833) referred by the same author to *V. arborescens*, which has since been transferred to *Calamites arborescens* (Sternb.) Kidston and Jongmans (1915). Later Geinitz (1855) and Feistmantel (1869) called it the fructification of *Asterophyllites foliosus* and finally the latter author (1872) believed it to be identical with *Macrostachya gracilis* Stur. The second species of Volkmannia originally described by Sternberg was *V. polystachya*. Apparently it is now referable to *Calamostachys polystachya* (Sternb.) Weiss (1884) although it has also been considered as the fructification of *Asterophyllites rigidus* and classified under the generic designations of Bruckmannia, Calamites, Paracalamostachys, Asterophyllites, and Palaeostachya.

According to the present rules of nomenclature Volkmannia, then, should be applied to the cones of the type which were originally described when this generic name was proposed. Calamostachys, which was created by Schimper (1869) for a portion of Volkmannia and which is now known to include Sternberg's original type material, must rightfully be reduced to synonymy. There is no justification for retaining a name of the basis of "euphony" (Seward, 1898, p. 351) nor on the basis of clarity as suggested by Schimper (1869). However, the long acceptance and present widespread, uniform application of the name Calamostachys, and the obvious implications of the relationship of this organ genus to Calamites may be sufficient grounds for recommending the retention of this name. In such a case, other forms which were erroneously included under the name Volkmannia may not retain this name, even after the complex assemblage of unrelated forms has been transferred elsewhere. Once the type material is removed from a genus, there is no further basis for retaining the name and it should then be considered a *nomen rejiciendum*. Therefore the inclusion under the name Volkmannia of various species now recognized as fructifications of Sphenophyllum, such as *V. Dawsoni*, cannot justify the retention of the name as valid for sphenophyllaceous fructifications.

The name Bowmanites was introduced in 1871 by Binney for the cast of a cone of uncertain affinity. He first believed the specimen *Bowmanites cambrensis* to be related, perhaps distantly, to Calamostachys. In his study he misinterpreted the sporangia, concluding that they were macrospores, but recognized sufficient distinctive characters to call it a new genus. In 1884, Weiss (pp. 200-202) substituted the generic name Bowmanites for Williamson's material called *Volkmannia Dawsoni*. This change to Bowmanites from Volkmannia was accepted by Williamson in 1890 (p. 99). He did so on the basis of proof furnished by Weiss (1884, p. 201 and pl. 21, fig. 12) that Weiss' new material, called *B. germanicus*, was undoubtedly comparable to Binney's figure for *B. cambrensis*, as well as to *B. Dawsoni*.

Later *B. germanicus* in turn was considered by Zeiller (1893) to be identical with *Sphenophyllum cuneifolium* cones, a correlation which seems tenable to most workers and with which we concur. The name Bowamnites was dropped by Williamson and Scott (1895) in favor of Shenophyllum after the rather conclusive proof by Zeiller that cones of *S. cuneifolium* were comparable to the petrified remains of *Bowmanites Dawsoni.*

Since that time several detached cones probably referable to the sphenophyllaceous vegetative remains have been described under the name Bowmanites; viz., *B. Römeri* Solms-Laubach (1895), *B. laxus* Halle (1927), *Bowmanites* species, Halle, (1927), and *Bowmanites* species, Kawasaki (1931). The recognition of Bowmanites by these competent workers, indicates their approval of that generic name at least for isolated fragments in preference to Sphenophyllostachys which was established later.

Seward introduced the name Sphenophyllostachys in the first volume of his "Fossil Plants" (1898, p. 402) as applicable to "Sphenophylloid cones which cannot be connected with certainty to particular species of Sphenophyllum." He admits the name Bowmanites has priority but justifies Sphenophyllostachys as being more tenable since it signifies cones belonging to Sphenophyllum. He cites the name Calamostachys as a similar logical example. We have already pointed out that Volkmannia has priority over Calamostachys and that mere convenience of terminology can not be admitted as a basis to overrule priority.

The name has been used by several authors in subsequent works and has recently come to be more generally accepted (Hirmer, 1927; Zimmerman, 1930; Walton, 1941). However on the basis of taxonomic priority and in recognition of the basic nature of fossil plant remains it is necessary to reestablish the name Bowmanites as proposed by Binney. The complete synonymy and emended description of the genus are given in the following section.

Taxonomic Treatment

Bowmanites (Binney) Hoskins and Cross, emend.

1871 *Bowmanites* Binney, Paleont. Soc. **1870**:59-60, pl. XII, figs. 1, 1a, 1b, 1c, 2, 3.
1822 *Sphenophyllites* Brongniart, Class. d. végét.. foss.: 9, 34; (pro parte).
1823 *Rotularia* Sternberg, Essai flora monde prim. **1**(2):34, 37; **1**(4):32; (pro parte).
1825 *Volkmannia* Sternberg, Vers. ein. geogn.-bot. Darst. d. Flora d. Vorwelt. Fasc. IV. I, **4**:42. Tentamen p. XXIX. (pro parte).
1828 *Sphenophyllum* Brongniart, Prodrome. p. 68. (pro parte).
1898 *Sphenophyllostachys* Seward, Fossil Plants **1**:401-402.
1909 *Monosphenophyllum* Lotsy-Vorl. ü. Bot. Stammesgesch. **2**:525, fig. 349, III.
1909 *Disphenophyllum* Lotsy—Ibid. **2**:525, fig. 349, IV.
1909 *Difurcosphenophyllum* Lotsy—Ibid. **2**:525, fig. 350, II:1, 2.
1909 *Tetrasphenophyllum* Lotsy—Ibid. **2**:525-526, fig. 350, III.

Fertile appendages of the Sphenophyllales, usually arranged in cones.

Sporophylls verticillate, either arranged in true cones or in a series of loose whorls alternating with vegetative leaves, borne terminally or on lateral branches, usually less than 2.5 cm. in diam. and 10 cm. in length, homosporous; compactly organized or lax, usually covered with the overlapping laminae

of successive whorls of sporophylls or sometimes only by peltate expansions of sporangiophores (*B. fertilis, B. Römeri* ?); axis small with small hexarch or triarch xylem surrounded by a weak parenchyma and a stronger outer cortex. Single vascular strands are given off at each point of the xylem which divide as they traverse the cortex in an upward direction to supply each leaf member of the whorl. Before entering the leaf the vascular bundle divides into an inferior (dorsal) strand which passes into the sterile bract and extends distally at least to its lamina (if present), and a superior (ventral) strand which may divide (probably dichotomously) once or twice to give rise to the individual vascular bundle which traverses the entire length of each sporangiophore and terminates abruptly at the point of attachment to the sporangium.

Sporophylls usually much modified, though some are indistinguishable from vegetative leaves, usually superimposed, always consisting of a sterile lower division and one to several, branched or unbranched, upper segment or segments, the sporangiophores, which bear distally small (0.5-3.0 mm.), elongate-ovoid (often distorted) sporangia, either singly, in pairs, or in groups, from infundibuliform or peltate expansions. Bases of sporophylls (bracts) fused into a collar-like disc in most species; tips free. Sporangiophores, though anatomically distinct when they emerge from axis, arise from the superior surface of the disc (fused bract bases) near the axis and bear their sporangia in one plane in one to several concentric cycles above each node (except *B. fertilis*).

Sporangial wall usually of two layers, the outer with large cells greatly thickened on their inner and lateral walls, the inner layer of two to four rows of delicate cells which appear to be continuous with the parenchyma of the sporangiophore. Sporangia densely packed with large numbers of isosporous spores which may vary slightly in size in the same species. Spores usually with a ridged (falsely spinose) perisporium; exine pustulose with triradiate tetrad scar extending less than half way to margins; intine delicate.

At present 18 species are recognized as valid; most species probably borne on plants known by leaf impressions or stem anatomy as Sphenophyllum.

The outstanding characters which delimit this genus from other allied genera (Calamostachys, Cheirostrobus, Cingularia, Palaeostachya, et al.) are its homospory, the division of sporophylls into a sterile lower portion and a fertile upper portion, the sporangiophore(-s), the pedicellate or stalked nature of the sporangia, the configuration of the spores and the triarch or hexarch nature of the xylem of the axis.

Known as compressions, casts and petrifactions from the Upper Paleozoic rocks of North America, Europe, Asia and the East Indies.

Bower and others (Bower, 1935, pp. 151-152; Seward, 1910, p. 7; Walton, 1940, p. 70) suggested that the organ genus for fertile shoots related to Sphenophyllum is heterogeneous and that certain forms should be removed from it in view of their apparent morphological differences. But after a careful investigation of most of the records of fertile shoots of Sphenophyllum and an analysis

of the group as a whole, we concluded that Bowmanites is a homogeneous organ genus and prepared the above generic description in accordance with this interpretation.

Further, on the basis of the number of sporangia borne on every sporangiophore, the species here included in the genus Bowmanites can be placed in the following three distinct sections, i.e., Simplices, Jugati and Conferti. Descriptions of these sections are given below and are followed by a key to the valid species, each of which is then described as fully as possible.

Section **Simplices** Hoskins and Cross, sect. nov.

Sporophylls arranged in distinct cones or alternating with sterile bracts from which they may or may not be distinguishable. Always one sporangium borne (often in an anatropous fashion) at the enlarged distal end of a more or less elongated sporangiophore; one to five sporangia per bract arranged in as many concentric verticels in one plane above each whorl of sporophylls.

Section **Jugati** Hoskins and Cross, sect. nov.

Sporophylls morphologically different from sterile leaves and always arranged in distinct cones. Sporangia borne in pairs on a distal, peltate expansion of the branched or unbranched sporangiophore. Two to thirty-four sporangia per sporophyll, often not arranged in a single plane but densely packed between two successive whorls of sporophylls.

Section **Conferti** Hoskins and Cross, sect. nov.

Sporophylls never arranged in distinct cones and often indistinguishable from sterile leaves. Sporangia borne in clusters of four on a terminal disc-like expansion of the sporangiophore. Four to eight sporangia (one to two clusters) per sporophyll arranged in a single plane above the sterile pedicel.

Key to the Species of Bowmanites

I Sporangia borne singly on sporangiophores ..... Section *Simplices*
A Mostly one or two (rarely three) sporangiophores per bract.
B Always one sporangiophore per bract and one whorl of sporangia per node.
C Sporangia borne on elongate sporangiophore ..... *B. simplex* (1)
CC Sporangiophore very short; sporangia appearing sessile.
D Sporangia borne axially; sporophylls moderately curved and short..... *B. trichomatosus* (2)
DD Sporangia borne somewhat distally on pedicel. Lamina of sporophyll vertical to pedicel and extended below it to form a spur or heel..... *B. angustifolius* (3)
BB Usually two sporangiophores per bract (sometimes one or three).
C Two (rarely one) whorls of sporangia per node. Cone small. Stele triarch in petrified specimens.
D Petrifactions; sporangiophores greatly elongated ..... *B. Scottii* (4)
DD Compressions; sporangiophores short.
E Cones small, compact; sporophylls much dissected. ..... *B. tenerrimus* (5)
EE Cones 5-8 cm. long, lax; sporophylls not dissected..... *B. gracilis* (6)

CC Two whorls of sporangia per node (sometimes three whorls on the same cone). Cones large, if present; stele hexarch in petrified specimens.
D Fertile bracts arranged in definite cones.
E Petrifactions. ..... *B. Dawsoni* (7)
EE Compressions.
F Westphalian A, B, and perhaps C. ..... *B. cuneifolius* (8)
FF Stephanian or Westphalian D. ..... *B. verticillatus* (9)
DD Fertile bracts not arranged in definite cones. ..... *B. charaeformis* (10)

AA Always three or more sporangiophores per bract. Sporangia always in three or more verticels in one plane per node.
B Three concentric verticels of sporangia per node. ..... *B. trisporangiatus* (11)
BB Four or more concentric verticels of sporangia per node. ..... *B. cambrensis* (12)

II Two or more sporangia borne on each sporangiophore.
A Sporangia borne in pairs on sporangiophores ..... Section *Jugati*
B Sporangiophores unbranched.
C Usually 3 per sporophyll. ..... *B. Römeri* (13)
CC Usually 1 per sporophyll. ..... *B. laxus* (14)
BB Sporangiophores much branched; 14-18 per sporophyll. ..... *B. fertilis* (15)
AA Sporangia borne in clusters of four on each sporangiophore ..... Section *Conferti*
B One sporangiophore per bract terminated by a large (one cm.) disc which bears the sporangia. ..... *B. Kidstoni* (16)
BB Two sporangiophores per bract terminated by a much reduced disc (sometimes only a point of coalescence of sporangia bases).
C Sporangiophores and groups of sporangia in two concentric whorls per node; arising serially on undivided bracts. ..... *B. major* (17)
CC Sporangiophores arising singly on adjacent halves of each bract, forming one concentric whorl of sporangiophores. ..... *B. tenuissimus* (18)

Description of Species

1. Bowmanites simplex Hoskins and Cross, spec. nov.

1877 *Sphenophyllum* sp. Renault, Ann. Sci. Nat. Bot., sér. 6, **4**:303-304, pl. 9, figs. 9-11.
1882 *Sphenophyllum* sp. Renault, Cours Bot. Fos. **2**:102-103, pl. 15, figs. 7-8, pl. 16, fig. 3.
1893 *Sphenophyllum* sp. Zeiller, Mém. Soc. Géol. France, Paléont. Mém. **11**:28-30, pl. V, figs. 5, 5A, 5B, 5C, 5D.
1893 *Sphenophyllum* sp. Zeiller, Ibid:34-36.

Cones very small, 11 mm. long x 3-5 mm. diameter. Subglobose sporangium borne singly on short sporangiophore which is attached to it as in *B. Dawsoni;* one per bract borne a short distance from axis. Spores very small; configuration unknown. Sporophylls inserted on the axis at an angle of 90°. Pedicels of sporophylls about 1 mm. in length and laminae arise vertically for about 2 millimeters.

One concentric whorl of sporangia above each whorl of bracts, the small size, and the prominent insertion of the sporophylls at right angles are the distinguishing features. This species also occurs much later geologically, i.e., Upper Carboniferous (Stephanian), than *B. Scottii* and *B. Dawsoni,* with which it may be most closely compared.

Stephanian (Grand 'Croix); silicified magmas near Saint-Étienne, France. Petrifactions (Only two specimens known).

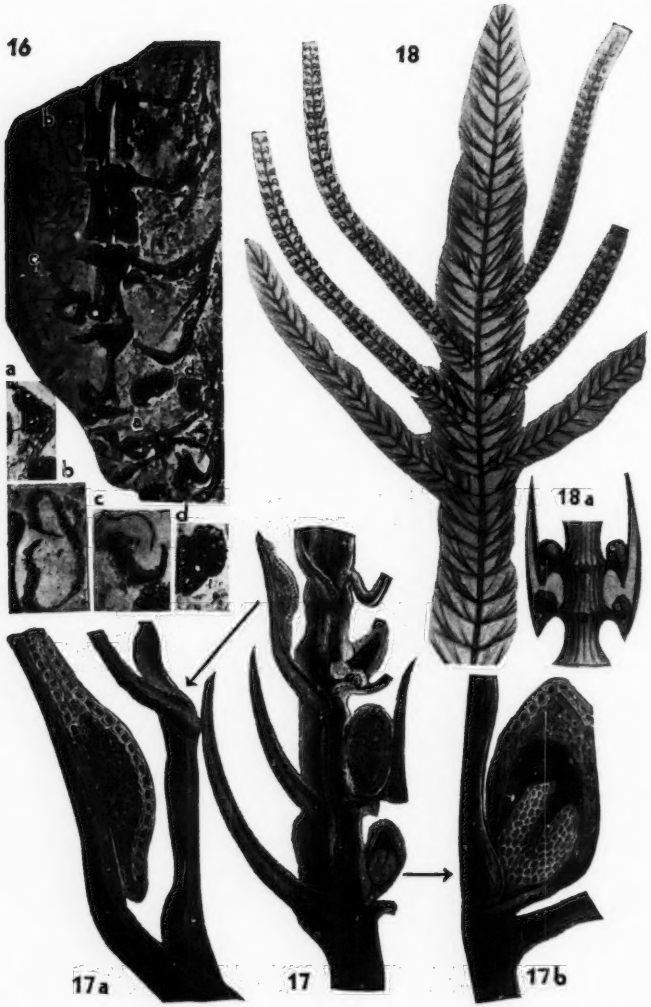

Fig. 16. Longitudinal (near radial) section of *Bowmanites simplex*. (After Zeiller, 1893). a, b, c, and d, are sections of the much broken and distorted sporangia.

Fig. 17. Holotype of *B. simplex* (After Renault, 1877). 17a shows a much flattened sporangium and a bract. 17b was interpreted by Renault as a megaspore. The peculiar

Holotype specimen: Figured by Renault, 1877, pl. 9, figs. 9-11.
Hypotype: Figured by Zeiller, 1893, pl. V, figs. 5, 5A, 5B, 5C, 5D.

2. **Bowmanites trichomatosus** (Stur) Hoskins and Cross, comb. nov.

1882 *Sphenophyllum tenerrimum* Weiss, Aus. Steink.: 12, pl. X, fig. 63; not Ett.
1884 *Sphenophyllum tenerrimum* Weiss emend., Abhandl. geol. Specialk. v. Preussen u. d. Thüringischen Staaten **5**(2):199, pl. XVI, figs. 4-5.
1887 *Asterophyllites trichomatosus* Stur. Abh. k. k. Geol. Reichsanst. Wien **11**(2):202, pl. 15, figs. 1-4.
1887 *Sphenophyllum trichomatosum* Stur, ibid.

True cones formed. Sporangia ovoid, borne singly and nearly sessile (probably borne on short sporangiophores) one per sporophyll, a short distance from the axis. Bracts or sporophylls not sharply bent up at distal extremities but rather gently curved from horizontal portion (pedicel). Usually considered to be sessile but better material may show sporangiophores present, a characteristic of the genus.

Carboniferous; Karwin, Karlsflötz; Dombrau. f. 2, 3.; Austria.

Yorkian (M. Coal-measures); Cooper's pit, Worsbro' Dale, Barnsley, Yorkshire. Shale and rock over Barnsley "Thick Coal" (Kidston's material).

Westphalian B; South Wales.

Suchaer (Upper Westphal. A); Ostrau-Kerwnir, etc.

Compressions.

Lectotype specimen: Figured by Stur, 1887, pl. 15, figs. 1-4.

This specimen found in connection with the foliage of *Sphenophyllum trichomatosum* Stur, but many subsequent records are of doubtful identity, the specimens being identified by vegetative characteristics without detailed study of the fertile appendages.

3. **Bowmanites angustifolius** (Germ.) Hoskins and Cross, comb. nov.

1848 *Sphenophyllites angustifolius* Germar, Verstein. Steink. Wettin u. Löbejün: 18, pl. VII, figs. 4-7.
1850 *Sphenophyllum angustifolium* Unger, Gen. et Sp. Plant. Foss.: 71.
1864 *Sphenophyllum angustifolium* (Ung.) Coem. and Kx. emend., Monographie Sphén.: 26, pl. 1. figs. 7, 7A, 7B.
1869 *Sphenophyllum angustifolium* (Germ.) Schimper, Traité Paléont. Végét. **1**:343-44, Atlas. pl. 25, figs. 1-4.
1882 *Sphenophyllum angustifolium* Germar, in Renault, Cours Bot. Fos.: 88-89, pl. 13, figs. 19-23.

Cones definite, lax, elongated (10 cm. ±), slender, borne as fertile lateral branches of indeterminate growth. One subglobose sporangium per bract borne

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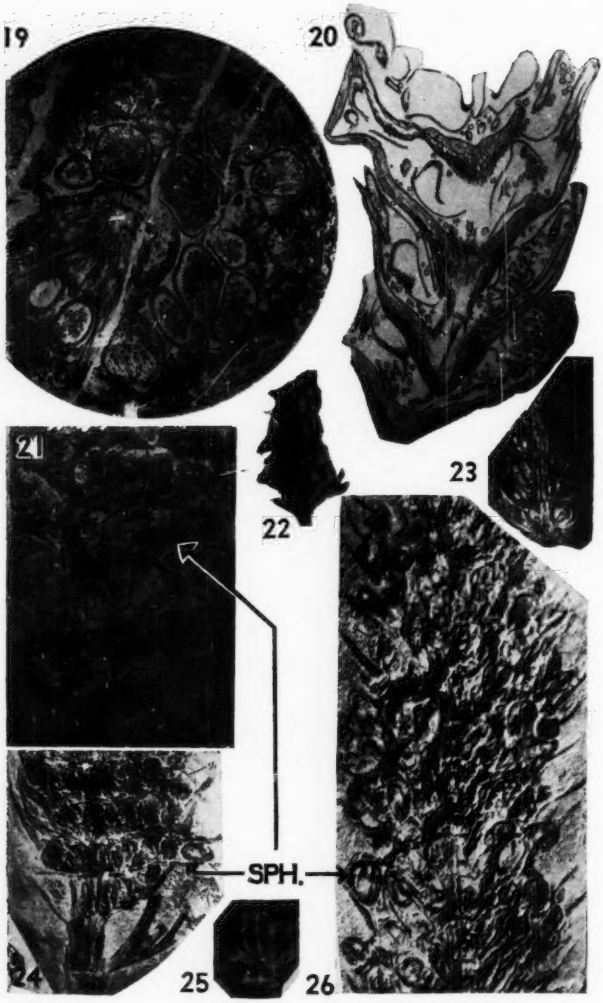
epidermal cells of the sporangium often present such a picture (see Fig. 5). Both these specimens were found by Renault though Zeiller studied the one shown in Fig. 16.

Fig. 18. *Bowmanites angustifolius* (Lectotype, after Schimper, 1874). Note the heel at the juncture between the end of the pedicel and the base of the lamina.



Figs. 19, 20. Obliquely transverse and longitudinal sections of *B. Scottii*. Lectotypes. (After Williamson and Scott, 1895).

Fig. 21. *Bowmanites gracilis*. Lectotype. Note sporangiophore (SPH) bearing sporangia in typical fashion. (After Zeiller, 1893).

Fig. 22. *B. tenerrimus* according to Stur. (After Renault, 1882).

probably on a short sporangiophore which is attached to the upper surface of the bract near the axis. (Possibly in older specimens the sporangiophore as well as the bract elongated and thus the sporangium itself is not borne in an axillary position but, rather, distally upon the pedicel). Distal portion of sporophyll pedicel appears cupped, having (externally) the appearance of a heel. Probably 6 bracts per whorl.

Upper Upper Carboniferous or Permian (Stephanian or Rotliegendes); South Wales, Germany.

Compressions.

Lectotype specimen: Figured by Schimper, 1874, pl. 25, figs. 1-4.

Usually associated with vegetative remains of *Sphenophyllum angustifolium*. An examination of these latter specimens indicate several species may be represented which cannot be distinguished on the basis of established criteria of leaves and stems.

4. **Bowmanites Scottii** Hoskins and Cross, spec. nov.

1895 *Sphenophyllum Dawsoni* (Will.) Will. and Scott, Phil. Trans. Roy. Soc. London, B, **185**:863-959, pls. LXXVI and LXXXV, figs. 26 and 54.
1898 *Sphenophyllostachys Dawsoni* (Will.) Seward, Fossil Plants **1**:401; (pro parte).
1908 *Sphenophyllum Dawsoni* (Will.) Will. and Scott, forma *beta* Scott. Studies in Foss. Bot., 2nd ed., **1**:100, 102-106, fig. 42.
1909 *Monosphenophyllum Dawsoni* (Will.) Lotsy, Vorl. über Bot. Stammesgesch. **2**:525, fig. 349, III. (pro parte).
1920 *Sphenophyllum Dawsoni* (Will.) Will. and Scott, forma *beta* Scott. Studies in Foss. Bot., 3rd ed., **1**:89, 92, 94, fig. 91.
1925 *Sphenophyllum Dawsoni* β. Will., in Leclercq, Mém. Soc. Géol. Belgique: 34.
1925 *Sphenophyllum Dawsoni* β. Schimp., in Leclercq, ibid. pl. VII, figs. 5, 5a.
1927 *Sphenophyllostachys Dawsoni* (Will.) Seward, forma β. Scott, in Hirmer, Handb. Paläobot. **1**:356-57, not. *Sph. Dawsoni* β of fig. 416.

Definite cones small, over 15 mm. long x 5.5 to 6.5 mm. in diam. Globose (sometimes distorted) sporangia (about 0.5-1.0 mm. in diam.) borne singly on elongated sporangiophores, 2 per bract (rarely one) in 2 concentric verticels between each two whorls of sporophylls. Sporangiophores slender (0.15 mm. in diam.) where they arise from the superior surface of sporophylls near the axis; inflated or swollen (0.4 mm. in diam.) where they join the sporangia. Sporangium suspended like an anatropous ovule in regard to its funiculus. Spores spherical, 65-85 μ in diam. including anastomosing ridges of perisporium which give a spinose appearance in section. Sporophylls about 15 per whorl, elongated, curving gently upwards distally and overlapping the laminae of several superior verticels; fused at base into narrow collar and inserted on the axis at the nodes at an angle of about 45°; about 5 whorls per centimeter of the axis.

Fig. 23. *Bowmanites* sp. Kawasaki (1931, Fig. 20). Possibly *B. simplex* or *B. trichomatosus*, but certainly a member of the Simplices.

Figs. 24-26. *Bowmanites cuneifolius*. Lectotype. (After Zeiller, 1893). The sporangiophores (SPH) and sporangia in two's on each bract show clearly. Fig. 25 shows a single whorl of bracts with sporangia removed showing cup-like fusion of the several sporophylls into a collar.

This species essentially similar in anatomy to *Bowmanites Dawsoni* (Will.) Weiss except for its triarch xylem (instead of hexarch), its smaller number of sporangia between each two whorls of bracts, and its generally smaller size.

Lower Coal-measures; Halifax, England.
Bouxharmont beds; Werister, Belgium.

Petrifactions.

Cotypes: Figured by Williamson and Scott, 1895, pl. LXXVI, fig. 26 (C. N. 1898, I.), and pl. LXXXV, fig. 54 (C. N. 1898, K.)

Associated with *Sphenophyllum plurifoliatum* Will. (= *S. myriophyllum* Crépin).

5. **Bowmanites tenerrimus** (Ett.) Hoskins and Cross, comb. nov.

1854 *Sphenophyllum tenerrimum* Ettingshausen, Abh. k. k. Geolog. Reichsanst. Wien. **2**(3):30-31; (pro parte).
1874 *Sphenophyllum tenerrimum* (Ett.) Helmhacker, Berg – und hüttenm. Jahrb. **22**(1): 50-53, pl. III, figs. 14, 15.
1877 *Sphenophyllum tenerrimum* (Ett.) Stur, Abh. k. k. Geol. Reichsanst. Wien **8**(2): 108 (214), pl. VII; text-figs. 21-24.

Cones compact, very small, terminal. Sporangia, probably on short pedicels, arranged in one or two concentric verticels per whorl of bracts; axillary in position. Essentially similar (though smaller) to *Bowmanites cuneifolius* but for one outstanding feature, i.e., the bracts are greatly dissected and ultimate segments are linear and ribbon-like as are those of the vegetative remains with which they are associated. A ridge or fold on the dorsal and distal side of the pear-shaped sporangia indicates position of sporangiophore.

Upper Upper Carboniferous; (Kulm) Austria.
Lower Namurian A; Silesia.

Compressions.

Lectotype: Figured by Helmhacker, 1874, pl. III, figs. 14-15.

Associated by direct connection with vegetative remains of *Sphenophyllum tenerrimum* (in part).

6. **Bowmanites gracilis** (Crépin) Hoskins and Cross, comb. nov.

1880 *Sphenophyllum gracile* Crépin, Bull. Soc. Roy. Bot. Belgique, sér. 2, **19**:8-10.
1893 *Sphenophyllum gracile* (Crépin) Zeiller, emend. Mém. Soc. Géol. France, Paléont. Mém. 11, **4**:25-26. Text-fig. H.

Cones, known only from impressions, lax, 5-8 cm. long, 3-5 mm. wide, probably covered with overlapping laminae. Ovoid sporangia borne singly on short, thick sporangiophores, probably 1 (sometimes 2) per bract in one or two concentric verticels between two whorls of 6 leaves each, per node. Morphologically these cones resemble those of *Bowmanites Scottii* and even the dimensions of comparable structures of the two agree fairly well with one another. The specimens studied by Zeiller seem to indicate that at least some of them were immature. The smaller number of bracts per whorl (6) as compared with

14 ± in *B. cuneifolius*, and the very distinct pedicels of the sporangia, as compared with the nearly sessile condition in *B. trichomatosus* are the delimiting features which justify its specific validity.

Carboniferous (Charbonnages des Produits); Belgium.

Compressions.

Lectotype: Figured by Zeiller, 1893, Text-fig. H. From Charbonnage des Produits.

Associated with vegetative remains described as *Sphenophyllum gracile* Crépin.

7. BOWMANITES DAWSONI (Will.) Weiss, Abhandl. geol. Specialk. v. Preussen u. d. Thüringischen Staaten **5**(2):200-202. 1884.

1871 (1876) *Volkmannia Dawsoni* Williamson, Mem. Lit. and Phil. Soc. Manchester, ser. 3, **5**:28-40, pls. I-III, figs. 1-7.
1893 *Sphenophyllum cuneifolium* Zeiller, Mém. Soc. Géol. France, Paléont. Mém. 11, **4**:1-39, pl. II, figs. 1-3, pl. III, figs. 1, 2; (pro parte).
1895 *Sphenophyllum Dawsoni* (Will.) Williamson and Scott, Phil. Trans. Roy. Soc. London, B, **185**:863-959, pl. LXXVI, fig. 25; pl. LXXXV, figs. 55-58; (pro parte).
1898 *Sphenophyllostachys Dawsoni* (Will.) Seward, Fossil Plants **1**:401; (pro parte).
1901 *Sphenophyllum cuneifolium* (Sternb.) Kidston, Trans. Nat. Hist. Soc. Glasgow **6**(1):124-27, fig. 23; (pro parte).
1908 *Sphenophyllum Dawsoni* (Will.) forma α Scott, Studies in Foss. Bot., 2nd ed., **1**:100, 102-106, fig. 43.
1909 *Monosphenophyllum Dawsoni* (Will.) Lotsy, Vorl. ü. Bot. Stammesgesch. **2**:525, fig. 349, III; (pro parte).
1914 *Bowmanites Dawsoni* Will., in Pelourde, Paléont. Végét.: 70.
1920 *Sphenophyllum Dawsoni* (Will.) forma α Scott, Studies in Foss. Bot., 3rd ed., **1**:92-96, fig. 46.
1927 *Sphenophyllostachys Dawsoni* (Will.) Seward forma α Scott et forma β Scott, in Hirmer, Handb. Paläobot. **1**:355-56, figs. 416-418; not *Sph. Dawsoni* (Will.) Seward forma β Scott, ibid.: 356, line 15 to end of page.
1940 *Sphenophyllum* (*Sphenophyllostachys*) *Dawsoni* (Will.) Williamson and Scott, in Walton, Study of Foss. Plants:70-72, fig. 47.

Cones large, 10-12 mm. or more in diam., several cm. long; axis 2.5 mm. diam.; hexarch xylem characteristic. Subglobose sporangia (sometimes distorted) borne singly, in an anatropous fashion (i.e., pendant and suspended on the sporangiophore from its adaxial side), usually 2, sometimes three per bract, disposed in two (or occasionally three) concentric verticels above each whorl of bracts; 1-2 mm. in diam. (±). Sporangiophores long, slender, 0.15 mm. in diam. where they become free from surface of bract and inflated (or infundibuliform) to about 0.4 mm. in diam. where they fuse with the wall of sporangia which is apparently one layer of cells thick. Spores, 75-100 μ in diam. (average for 12 specimens) including ridged perisporium, appear spinous in cross section and possess a triradiate scar on exosporium. Sporophylls (bracts) 14-20 per whorl fused into a collar at their bases, inserted at an angle of about 60° and curving gently upward; laminae overlapping several superior whorls; bundle divides upon entering collar of fused bracts giving rise to a strand for its respective bract and another strand which bifurcates again and supplies the two sporangiophores.

The special features of this species are the large size of its cones, the presence in most cases of two sporangiophores per bract, and the hexarch xylem. By comparison *B. Scottii* has smaller cones and a triarch xylem, wheras *B. trisporangiatus* is generally larger and has ordinarily three whorls of sporangia per node.

Lower Coal-measures; Halifax, Oldham, Shore, Stalybridge and Bacup, Great Britain.

Finefrau-Nebenbank; Netherlands.

Petrifactions.

Lectotype: Figured by Williamson (1876), pls. I-III, figs. 1-7 (C. N. 1049, etc.)

Associated indirectly but rather conclusively with vegetative remains of *Sphenophyllum cuneifolium.*

8. **Bowmanites cuneifolius** (Sternb.) Hoskins and Cross, comb. nov.

1823 *Rotularia cuneifolia* Sternberg, Versuch I. Fasc. II:33, pl. XXVI, figs. 4a and 4b.

1880 *Sphenophyllum cuneifolium* (Sternb.) Zeiller, Végét. foss. du terr. houil. de la France: 30, pl. CLXI, figs. 1, 2. (pro parte).

1884 *Bowmanites germanicus* Weiss, Abhandl geol. Specialk. v. Preussen u. d. Thüringischen Staaten **2**:201 (287), pl. XXI, fig. 12.

1893 *Sphenophyllum cuneifolium* (Sternb.) Zeiller, Mém. Soc. Géol. France, Paléont. Mém. 11, **4**:1-39, pl. I, pl. II, figs. 1-3, pl. III, figs. 1-2.

1911 *Bowmanites germanicus* Jongmans, Meded. Ryks. Ops. van Delfs **3**:417, fig. 391.

Cones definite, lax, more than 1 cm. in diam. and up to 10 cm. in length. Known as compressions from essentially the same horizons as *B. Dawsoni* and possibly identical with it. Two (sometimes three) concentric whorls of sporangia borne on elongated pedicels which arise from the superior surfaces of the 14-20 bracts which are fused into a collar or cup at their bases, and are extended vertically, their linear lanceolate tips overlapping several superior whorls.

The specimens of Weiss and Jongmans, i.e., *B. germanicus* Weiss, are somewhat smaller than the cones usually found on undoubted *Sphenophyllum cuneifolium* stems and the sporangia are markedly smaller but they are possibly immature. Because the petrified specimens of undoubted *B. Dawsoni* have not been found in connection with vegetative parts of *Sphenophyllum cuneifolium* Sternb., it is best not to combine here that species with *Bowmanites cuneifolius.*

Midddle and Lower Coal-measures; Great Britain.

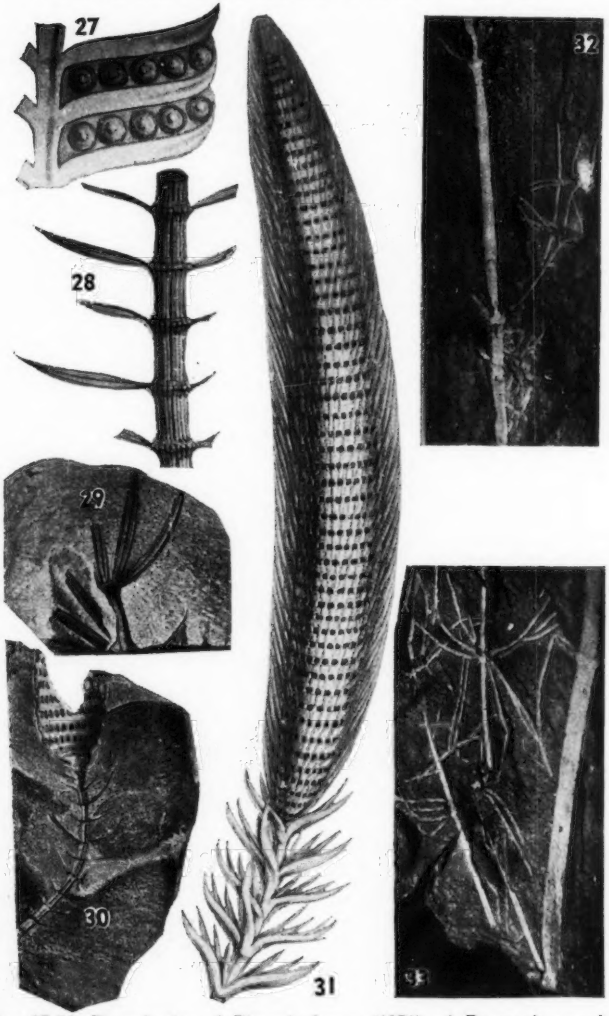
Westphalian A; French and Belgian coalfields.

Middle and Lower Coal-measures; Great Britain.

Compressions.

Lectotypes: Figured by Zeiller, 1893, pl. I, figs. 1, 1b, 2, 2a, 3, 4, 4a; pl. II, fig. 2a.

Associated by organic connection with vegetative remains of *Sphenophyllum cuneifolium.*



Figs. 27-31. Reproduction of Binney's figures (1871) of *Bowmanites cambrensis*. Lectotype. Fig. 27. The ten sporangia in this figure were interpreted as spores by Binney. Fig. 30 shows a photo of a mold of the base of the cone and Fig. 31 is a reproduction of a drawing made by Mr. Bowman when he had all the fragments of the cone at hand.

Figs. 32-33. *Bowmanites charaeformis* Jongmans (1912) (lectotype); showing lax nature of vegetative branch and the long, unmodified leaves which bore the sporangia in their axils.

9. **Bowmanites verticillatus** (Schloth.) Hoskins and Cross, comb. nov.

1804 *Sphenophyllum verticillatum* Schlotheim, Flora d. Vorwelt: 57, pl. 2, fig. 24.
1837 *Sphenophyllites Schlotheimii* Germar, Isis: 425, pl. 2, fig. 1, a, b.
1855 *Sphenophyllum emarginatum* Brongt., *in* Geinitz, Die Verst. der Steink. form. in Sachsen: 12, pl. 20, fig. 7.
1883 *Sphenophyllum emarginatum* Brongt., in Schenk, Pflanz. Verst. Richt. "China" **4**:220, pl. XXXVIII, fig. 1.
1910 *Sphenophyllum verticillatum* Schloth., in Zobel, *in* Potonié, Abb. und Beschr. No. **138**:1-10, figs. 1-7.

Two types of cones postulated; if actually present, this species would be the only established heterosporous member of the genus. Female cones similar in structure to the cones of *Bowmanites cuneifolius* (scarcely distinguishable from the immature specimens of the latter). Male cones with numerous sporangia (0.5 mm. in diam.) crowded in several axillary verticels at each node. The spores of these are supposedly round and without ornamentation. The other (female?) sporangia are elongated, axillary, 1 mm. in diameter, and equal in number to that of the subtending bracts, and contain macrospores (No spores have been illustrated).

We believe that further investigation will reveal that the two forms are actually separate species or that the "microsporangiate" cone is very immature. This would account for the smaller size, and the unornamented (immature) spores, but not the extra whorls of sporangia which are more difficult to explain.

Though tentatively separated this species seems to belong, at least in part, to *B. cuneifolius* ("microsporangiate" cones), whereas the remainder belongs possibly to *B. trichomatosus* ("macrosporangiate" cones), or an unknown similar form.

Upper Carboniferous; Lititz near Pilsen, Bohemia.
Stephanian or Westphalian D; Germany, Russia, et al.

Compressions.
Associated indefinitely with remains of *Sphenophyllum verticillatum* Schloth.

10. **Bowmanites charaeformis** (Jongmans) Hoskins and Cross, comb. nov.

1912 *Sphenophyllum charaeforme* Jongmans, Ann. k. k. Nat. Hofmus. Wien **1912**: 449-450, pl. 6.

No definite cones present. Sporangia borne in anatropous fashion singly at the slightly enlarged tips of slender sporangiophores. Two sporangiophores or more arise from the ventral (adaxial) surface of each bract near the axis. Fertile leaves or bracts similar in appearance to sterile leaves and of same number (9?) per whorl. Vegetative stems are slender, 1-2 mm. in diam., with long (3 cm. ±) internodes; lateral branches, with internodes 2 cm. long, bear fertile leaves at their nodes.

Jongmans noted a longitudinal ridge on the surface of several sporangia which suggested to him a possibility that a fused pair of sporangia instead of a single one were borne terminally on each sporangiophore. Unless this condi-

tion is definitely established, *B. charaeformis* must be placed in the section *Simplices*.

Lower Upper Carboniferous, Franziska vein, Ostrau section; Hruschau, Lower Silesia.

Compressions.

Lectotype: Figured by Jongmans, 1906, pl. 6.

Associated with vegetative remains of *Sphenophyllum charaeforme* Jongmans.

11. **Bowmanites trisporangiatus** Hoskins and Cross, spec. nov.

Definite cone larger than those of *B. simplex, B. Scottii,* and *B. Dawsoni;* not less than 16 mm. diam. and several (6±) cm. long. Axis over 4.5 mm. in diam. Vascular cylinder of axis unknown. Three, essentially spherical, large (1.7-2.4 mm. diam.) sporangia borne singly in an anatropous manner above each of the 18 bracts of each whorl; always appearing as three concentric series or verticels of sporangia above each whorl of sporophylls. Sporangial wall two-layered with an outer single layer of large cells and an inner multicellular layer of delicate cells. Spores large, 100-150 μ including irregular perisporium of anastomosing ridges with bipolar orientation (central body of spore 75- 125 μ). Exine pustulose or granular with prominent tri-radiate tetrad scar. Spores densely packed in sporangia. Sporangiophores slender (250 μ), greatly elongated, separated at their bases, arising in three distinct positions near the axis from the surface of the collarette formed by the laterally fused bases of the bracts; infundibuliform at distal end from which sporangium is suspended. Sporophylls inserted at an angle of about 60°; laminae turned abruptly upward at distal end of pedicels and overlapping several (?) whorls above. Single bundle bifurcates in outer cortex, the dorsal (inferior) strand supplying the bract and the ventral (superior) strand giving rise to three branches, in two simultaneous divisions, which are separate and surrounded by parenchymatous tissue and appear as ridges fused to the surface of the bract at the point of emergence from the outer cortex.

The characteristic and constant occurrence of three sporangia per bract in three concentric whorls per node in any section, in addition to the larger size of spores and cone in general, are the principal features which distinguish this pecies. The known geologic occurrence is markedly later than that of *B. Dawsoni, B. Scottii, B. cuneifolius,* but somewhat earlier than that of *B. simplex.*

Upper Carboniferous, Des Moines Series (= Lower Carbondale of Illinois = Lower Allegheny of Eastern U. S. = Upper Westphalian C of Europe); Oskaloosa, Mahaska County, Iowa.

Petrifaction.

Holotype: One specimen from Des Moines Series, Iowa. University of Cincinnati Paleobotanical collection No. 1706 A-T.

Vegetative associations unknown.

12. **Bowmanites cambrensis** (Binney) Hoskins and Cross, emend.

1871 *Bowmanites cambrensis* Binney, Paleont. Soc.: 59. pl. XII, figs. 1, 1a, 1b, 1c, 2, 3.

1888 *Bowmanites cambrensis* (Binney) Howse, Cat., Nat. Hist. Trans. of Northumberland, etc. **10**:38, fig. 2.

1893 *Sphenophyllum cuneifolium* (Sternb.) Zeiller, Mém. Soc. Géol. France, Paléont. Mém. 11, **4**:3-39. (pro parte).

1927 *Sphenophyllostachys Dawsoni* (Will.) Seward, forma *gamma* Hirmer, Handb. Paläobot. **1**:357. figs. 419, 420.

Large cones about 10 cm. long and 1-2 cm. in diam., borne at tips of lateral branches. Essentially similar in structure to *B. Dawsoni* but with 4-5 pedicellated sporangia per bract and consequently 4-5 concentric whorls of sporangia between each internode. Probably all sporangia borne linearly upon the bract and not in alternating groups of one and two as postulated by Hirmer. Sometimes displaced to the one or the other side of the bract if not in linear arrangement.

About 24 bracts per whorl whose attenuated laminae overlap characteristically the superior whorls forming a bristly sheath as in nearly all cones of the Sphenophyllales.

Lower Coal-measures; near Pontypool, S. Wales, and Bensham Seam; Jarrow.

Casts and Compressions.

Lectotype: Figured by Binney, 1871, pl. XII, figs. 1-3.

Vegetative associations indefinite.

13. BOWMANITES RÖMERI Solm-Laubach, Jahrb. d. d. k. Geol. Reichsanst. Wien **45**(2):225, pl. IX. figs. 1-4, pl. X. figs. 1-10. 1895.

1898 *Sphenophyllostachys Römeri* (Solms-Laub.) Seward, Fossil Plants **1**:405, figs. 107c, 107d.

1901 *Sphenophyllum Römeri* (Solms-Laub.) Kidston, Trans. Nat. Hist. Soc. Glasgow, n.s., **6**(1):127-8. fig. 24.

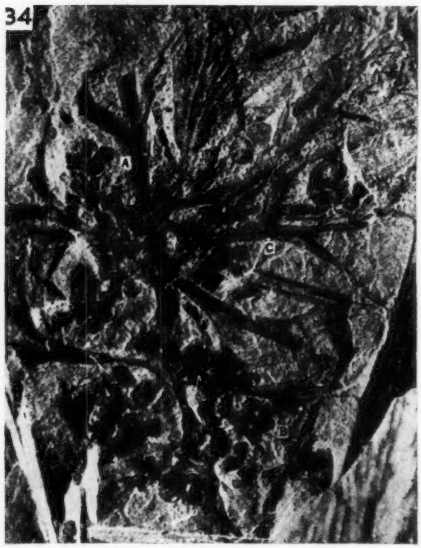
1909 *Disphenophyllum Römeri* (Solms-Laub.) Lotsy, Vorl. ü. Bot. Stammesgesch. **2**:525, fig. 349, IV.

1920 *Bowmanites Römeri* Solms-Laub., in Scott, Studies in Foss. Bot., 3rd ed., **1**:96-99, figs. 48, 49.

1927 *Sphenophyllostachys* (*Bowmanites*) *Roemeri* (Solms-Laub.) Seward, in Hirmer-Handb. Paläobot. **1**:357. figs. 421-23.

1940 *Bowmanites Römeri* Solms-Laub., in Walton, Study of Foss. Plants: 73.

Well developed cones, approx. 1 cm. in diam.; length several cm. (indefinite); axis unknown. Sporangia elongate-ovoid, 1-2 mm. long with wall several cells in thickness, attached in pairs by their abaxial side to the peltate tip of the slender, elongated sporangiophore; 6 per bract on 3 unbranched sporangiophores (appearing as 3 concentric verticels of sporangia per whorl of bracts in radial sect. of the cone as in *B. trisporangiatus*). All 3 sporangiophores arise from surface of the bract, probably from a point near the axis. Spores nearly



Figs. 34-35. *Bowmanites major* showing the grouping of sporangia in two groups of four each per bract. (After Kidston, 1911, text-fig. 35). Lectocotype, No. WH 2172, Kidston coll.

Fig. 36. *B. tenuissimus*. Lectotype. A much smaller plant than *B. major*. Note the broken group of four sporangia at "a." (After Kidston, 1914).

Figs. 37-39. *B. laxus* Haile. Figs. 37 and 39 show rather clearly one sporangiophore bearing two sporangia per bract.

spherical, 100 μ in diam. densely crowded, with two walls, the exine membranous and often folded, the perisporium thick and bearing numerous anastomosing ridges. Sporophylls separate almost to base (number per whorl unknown); arranged in superposed whorls with the narrow tips overlapping several whorls above.

Middle Upper Carboniferous; Niedzielisko, near Cracow, Poland.

Petrifaction (only one specimen known.)

Lectotype: Figured by Solms-Laubach, 1895, pl. IX, figs. 1-4; pl. X, figs. 1-10.

Vegetative associations unknown.

14. BOWMANITES LAXUS Halle, Paleont. Sinica, A, 2(1):52-54, pl. 11, figs. 1-4. 1927.

Well developed cones, over one cm. in diam., more than 5 cm. long; axis thick (4 mm. in diam.); prominent longitudinal ridges, opposed at the nodes, i.e., not alternating; internodes less than 3 mm. in length. Sporangia subglobose, 1.0-1.5 mm. in diam., attached in pairs by their abaxial side to the peltate tip of the slender, elongated (2.5 mm.) sporangiophore; 2 (rarely 4) per bract on 1(2) unbranched sporangiophores (usually appearing as one verticel of sporangia per whorl of bracts in a radial section of the cone). Sporangiophore appears to arise from the surface of each bract in an almost axillary position. This condition plus the peltate, bisporangiate tip, recall *Cingularia*. Spores unknown. Sporophylls or bracts confluent for about half their length (forming the characteristic disc) which is about twice the diameter of the length of the internodes. Tips of individual bracts free, subulate, and often perpendicular to the axis; only occasionally recurved and nearly parallel with it, and rarely ascending to the base of the superior whorl of bracts.

Several cones borne on the thick axis (possibly that of *Sphenophyllum Thonii*) as lateral appendages at each node.

The single verticel of paired sporangia per bract, and the lack of overlapping of the shorter sporophylls which are also more broadly fused laterally, differentiate this species from *B. Römeri*. Additional material from China collected in a slightly younger stratum (Middle Shihhotse Series, Bed 31) and figured by Halle (1927, pp. 54-55, pl. 11, figs. 5-8) appears to belong to this species, but careful study of the original material would be necessary to establish this relationship.

Lower Permian (Lower Shihhotse Series); Chenchieyu, (East section: plant bearing bed 14).

Compressions.

Lectotype: Figured by Halle, 1927, pl. 11, figs. 1-4.

Associated questionably with *Sphenophyllum Thonii* Mahr.

15. **Bowmanites fertilis** (Scott) Hoskins and Cross, comb. nov.

1906 *Sphenophyllum fertile* Scott, Phil. Trans. Roy. Soc. London, B, **198**:17-40, pls. III-V, text-figs. 1-3.
1909 *Difurcosphenophyllum fertile* (Scott) Lotsy, Vorl. ü. Bot. Stammesgesch. **2**:525, fig. 350, II, 1, 2.
1927 *Sphenophyllostachys fertilis* (Scott) Hirmer, Handb. Paläobot. **1**:357, 359, figs. 424-25.
1936 *Sphenophyllum fertile* (Scott) Leclercq emend., Ann. Soc. Géol. Belgique **59**: 222-248, pls. I-X.
1936 *Sphenophyllostachys fertile* (Scott) Hirmer, in Leclercq Proc. Sixth Int. Bot. Cong. **1**:234, 239.
1937 *Sphenophyllum fertile* (Scott) Leclercq, Ann. Soc. Géol. Belgique **60**:170-172, figs. 1-4.

Definite compact cones present; at least 6 cm. long by 1-2.5 cm. in diam., not covered by sporophyll laminae. Sporangia ellipsoidal, 1.5-2.5 x 1-1.5 mm., surrounded by a single layer of cells with radially thickened walls; 2 per sporangiophore branch (bisporangiate) and 22-34 per sporophyll, densely crowded. Spores ellipsoidal, 90-96 x 65-70 μ, without heavily ridged perispore. Each node bears 6 sporophylls divided into 18 bracts, which are slightly fused at their bases; 6 of them ventral (adaxial), fertile and forked; 12 dorsal (abaxial), sterile, unbranched and lacking upturned portions; 14-18 sporangiophores inserted on the superior face of each fertile bract; each sporangiophore bearing terminally a more or less peltate expansion; some are sterile. Whorls of sporophylls superposed and partially covered externally by peltate sporangiophore tips.

Lower Coal-measures; Shore Littleborough, Lancashire.

Bouxharmont Beds; Assise de Châtelet, Belgium.

Petrifactions.

Lectotype: Figured by Scott, 1906, pls. III-V, text-figs. 1-3.

Vegetative associations unknown.

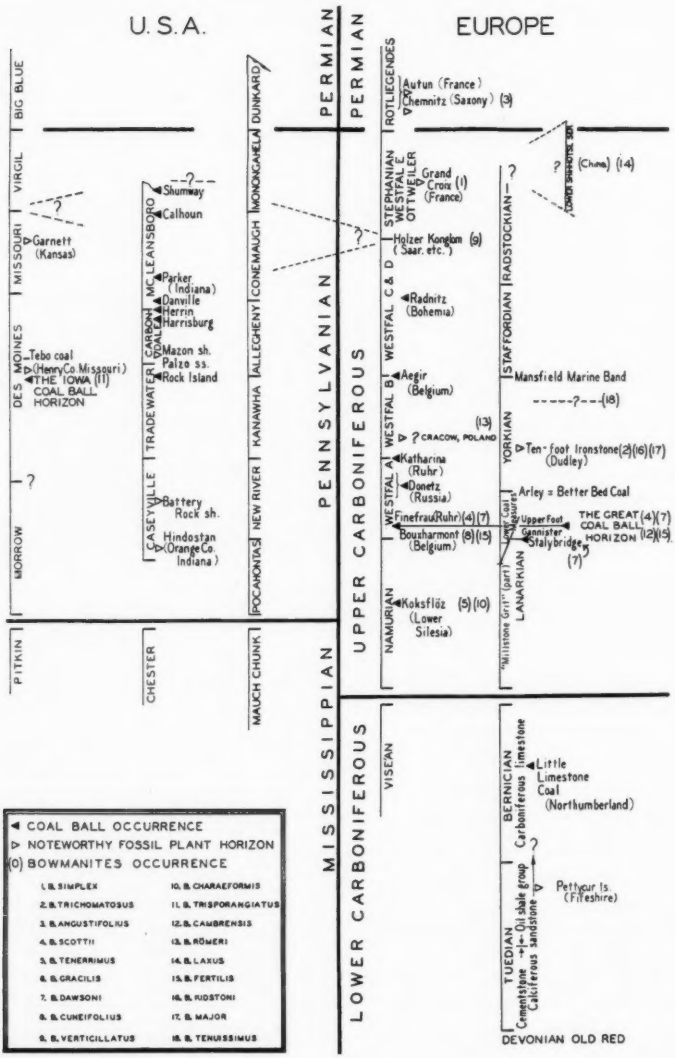
16. **Bowmanites Kidstoni** (Hem.) Hoskins and Cross, comb. nov.

1914 *Sphenophyllum* sp. Kidston, Trans. Roy. Soc. Edinburgh **50**:131, pl. X, figs. 5, 5a.
1931 *Sphenophyllum Kidstoni* Hemingway, Ann. Bot. **45**(177):41-44, pls. II, III, figs. 1-8, 17, text-fig. 2.

Definite cones absent. Sporangia occur in fours (tetrasporangia) irregularly among foliage in one whorl per node. Sporangia 1.1 mm. in diam., oval or "fig-shaped," i.e., broader than long and flattened at apex. Sporangiophore very short, attached to underside of broad (1.0 mm.) disc, which bears sporangia, and arises from collarette near axis (not clearly seen). 6 leaves per node, very deeply dissected (4-7 teeth).

Smaller than *B. major* and larger than *B. tenuissimus*.

Mid-Yorkian Series (Barnsley Coal, "Monckton Rock,"); Royston, near Barnsley. Yorkshire Coal Field (also Staffordshire coal field). Spec. nos. WH 2154, WH 2155, WH 2158, etc.


U. S. A.
EUROPE
PERMIAN
PERMIAN
PENNSYLVANIAN
UPPER CARBONIFEROUS
MISSISSIPPIAN
LOWER CARBONIFEROUS
BIG BLUE
VIRGIL
MISSOURI
DES MOINES
MORROW
PITKIN
CHESTER
MAUCH CHUNK
POCAHONTAS
NEW RIVER
KANAWHA
ALLEGHENY
CONEMAUGH
MONONGAHELA
DUNKARD
ROTLIEGENDES
STEPHANIAN
WESTFAL E
OTTWEILER
WESTFAL C & D
WESTFAL B
WESTFAL A
NAMURIAN
VISEAN
RADSTOCKIAN
STAFFORDIAN
YORKIAN
LANARKIAN
BERNICIAN
TUEDIAN
DEVONIAN OLD RED
Autun (France)
Chemnitz (Saxony) (3)
Grand Croix (1) (France)
Holzer Konglon (9) (Saar, etc.)
Radnitz (Bohemia)
Aegir (Belgium)
CRACOW, POLAND (13)
Katharina (Ruhr)
Donetz (Russia)
Finefrau Ruhr (4) (7)
Bousharmont (8) (15) (Belgium)
Koksflöz (5) (10) (Lower Silesia)
(China) (14)
Mansfield Marine Band (18)
Ten-foot Ironstone (2) (16) (17) (Dudley)
Arley = Better Bed Coal
Upper Foot
Gannister
Stalybridge
THE GREAT COAL BALL HORIZON (12) (15)
(7)
Millstone Grit (part)
Little Limestone Coal (Northumberland)
Pettycur ls. (Fifeshire)
Cementstone → ← Oil shale group
Calciferous sandstone
Garnett (Kansas)
Tebo coal (Henry Co. Missouri)
THE IOWA (11) COAL BALL HORIZON
Shumway
Calhoun
Parker (Indiana)
Danville
Herrin
Harrisburg
Mazon sh.
Palzo ss.
Rock Island
Battery Rock sh.
Hindostan (Orange Co. Indiana)
McLEANSBORO
CARBONDALE
TRADEWATER
CASEYVILLE
COAL MEASURES
COAL MEASURES
COAL MEASURES

Compressions.
Lectotype: Figured by Hemingway, 1931, pls. II, III, figs. 1-8, 17; text-fig. 2.
Vegetative associations uncertain.

17. **Bowmanites major** (Kidston) Hoskins and Cross, comb. nov.

1828 *Rotularia major* Bronn, in Bischoff, Die Kryptogamischen Gewächse **2**:139, pl. XIII, figs. 2a, 2b.
1835 *Sphenophyllum majus* Bronn, Lethoea Geol. **1**:32, pl. VIII, figs. 9a, 9b.
1901 *Sphenophyllum majus* Kidston, Trans. Nat. Hist. Soc. Glasgow. n. s. **6**(1):128-129, fig. 25. (Fructification).
1909 *Tetrasphenophyllum majus* (Kidston) Lotsy, Vorl. ü. Bot. Stammesgesch. **2**:525-26, fig. 350, III.
1931 *Sphenophyllum majus* (Bronn) Hemingway emend., Ann. Bot. **45**:39-40, pl. III, figs. 16, 16a, and text-figs. 1, A, B, and C.

No definite cones developed. Sporangia occur in fours (tetrasporangia) irregularly on leaf bracts, the whorls of which may alternate with similar whorls of sterile leaves. Sporangia about 1.5 mm. in diam., pyriform, attached to a much reduced central disc (sometimes only a point) or place of confluence of their attachment to the long slender sporangiophore which arises on the free surface of the fused collar (formed by lateral confluence of bract bases) near the axis. Two sporangiophores and two groups of four sporangia per bract form 2 concentric rings of sporangial groups per whorl, but may often be much displaced. The plant is larger than *Bowmanites Kidstoni* which it resembles closely.

Mid-Yorkian Series. (Shale over Barnsley Thick Coal); near Barnsley. Yorkshire coalfield. Spec. Nos. WH 855, WH 2172, etc.

Compressions.
Lectocotypes: Kidston's specimens Nos. WH 2172 (1911, fig. 35) and WH 855: Refigured by Hemingway, 1931, pl. III, figs. 16, 16a; text-figs. 1, A, B, C.
Associated with vegetative remains known as *Sphenophyllum majus* Bronn.

18. **Bowmanites tenuissimus** (Kidston) Hoskins and Cross, comb. nov.

1914 *Sphenophyllum tenuissimum* Kidston, Trans. Roy. Soc. Edinburgh **50**:129, pl. XVI, figs. 3, 4, 4a, 5, text-fig. 6.

Definite cones absent. A sporangiophore arises from each half of the divided fertile leaves which are morphologically similar to sterile leaves. Four small (less than 1 mm. including basal stalk), pyriform sporangia are borne on the disc-like terminal end of the sporangiophore. The disc is reduced almost to a point in this species. (The disc may be formed from the confluence of the much shortened, stalk-like attachments of the sporangia). The portion of the plant bearing the fertile leaves is very slender (stem, 1 mm. in diam.), several centimeters long and has long (7 mm.) internodes.

Middle Upper Carboniferous (Westphalian Series); Cosely near Dudley, Clayscroft, England.

Compressions.

Lectotype: Figured by Kidston, 1914, pl. XVI, figs. 3, 4, 4a, 5; text-fig. 6.

Associated with vegetative remains referred to *Sphenophyllum tenuissimum* Kidston.

Summary

1. An incomplete petrified strobilus found in a coal ball from the Des Moines Series in Iowa is here described as a new species, *Bowmanites trisporangiatus* Hoskins and Cross.

2. A detailed description of the structure is correlated with the general knowledge of related cones.

3. The genus Bowmanites (Binney) Hoskins and Cross is reestablished for isolated fragments and attached specimens of cones generally related to the organ genus Sphenophyllum (exclusive of Cheirostrobus), and an emended generic diagnosis is given.

4. Three sections of the genus Bowmanites are created, Simplices, Jugati, and Conferti.

5. Two new species, *Bowmanites simplex* Hoskins and Cross and *B. Scottii* Hoskins and Cross are established to receive some previously reported material, and eleven new specific combinations are made.

6. The old species *B. Dawsoni* is divided into three distinct species and the description of *B. cambrensis* is emended.

7. A key to the eighteen recognized species is included and new descriptions, as complete and uniform as possible, and the synonymy are given for each.

8. Taxonomic problems related to the naming of isolated or attached fossil plant fragments are discussed.

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Studies on the Nutrition of Collybia velutipes (Curt.) Quel. (Homobasidiomycetes, Agaricales)[1]

Brother Raphael Marczynzski, C.S.C.[2]

The agaricaceous fungus *Collybia velutipes* is causally related to decay of heartwood in stumps and in living trees. Cultures of the organism thrive on media prepared from natural products but do not develop well on a synthetic medium composed of glucose and the usual inorganic salts. This type of behavior indicates, as in many other fungi (Robbins and V. Kavanagh, 1942), that the natural products act as sources of vitamins. For this reason the vitamin deficiencies of *C. velutipes* were investigated. The results obtained are presented in this paper.

The strain of *C. velutipes* used in this study was an isolate from a sporophore collected from a stump of an elm tree in the vicinity of Notre Dame, Indiana. Stock cultures of the fungus were maintained in test tubes containing potato dextrose agar slants. Transfers from these cultures to Petri dishes containing 10 ml. of the same medium served as material for preparing inocula for the experimental media. The inoculum in each case consisted of an agar disk (2 mm. in diameter and 2 mm. thick) cut from the margin of a week old culture and containing several young hyphae. The variation in the weight of these small disks was considered to be too small to introduce appreciable error.

The vitamin deficiencies of the fungus were determined by observing the effect produced by vitamins added to a vitamin-free basal medium. The latter had the following composition: sucrose 34.2 gm., ammonium tartrate 9.2 gm., potassium dihydrogen phosphate 6.8 gm., magnesium sulphate (heptahydrate form) 2.5 gm., ferric chloride (one per cent solution) 0.6 ml., and distilled water 1,000 ml. Each of these ingredients was of reagent grade. The basal medium was dispensed in pyrex flasks, 25 ml. to each flask, to which the various vitamin supplements were added. These were supplied in the form of stock solutions prepared in such concentrations that one milliliter furnished the desired quantity of vitamin. The controls received one ml. distilled water. The total amount of medium in each flask was 26 ml.

The flasks were then stoppered with cotton, autoclaved at 13 pounds pressure for 20 minutes, cooled, the hydrogen-ion concentration of the medium

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2 Died February 11, 1943.

was determined, and the flasks were inoculated by hyphae-bearing agar disks and incubated at 25°C for 21 days. At the end of the incubation period the mycelium was collected on weighed filter papers, washed with distilled water, air-dried for 24 hours, oven-dried at 65°C for 24 hours, put in a desiccator over calcium chloride for at least 30 minutes and then weighed on an analytic balance.

Results and Discussion

The first set of experiments deals with the response of *C. velutipes* to crystalline thiamin, pyrimidine, thiazole, riboflavin, pyridoxine, and a concentrate of biotin. These vitamins were used in a wide range of concentrations and were employed singly and in various combinations. The results are presented in Table 1 (see also Fig. 1).

Thiamin greatly increases dry matter production. Dosages as low as 0.0001 gamma per 26 ml. of medium are active, inducing a 100 percent increase in dry matter. The optimal dosage is approximately 0.5 gamma per 26 ml. of medium. This dosage brings about an increase in dry matter production from 4.6 ± 0.9 mg. in the control to 19.6 ± 0.6 mg. in the vitamin supplemented medium, an approximate 400 per cent increase.

The thiamin components, thiazole and pyrimidine, are both active, increasing considerably the dry matter produced over that present in the control. The fact that *C. velutipes* grows appreciably in a medium containing no added vitamins is interpreted as indicating that a certain amount of thiazole and pyrimidine is synthesized. Only a very little thiazole is produced as is shown by the marked response to additions of this factor. The addition of thiazole is actually as effective as the addition of the entire molecule of thiamin. This indicates further that pyrimidine is present in amounts sufficient for the construction of optimal concentrations of thiamin. On the basis of these facts, one might expect additions of pyrimidine alone to be ineffective. This, however, is not the case. The data show that this component increases somewhat the dry matter production, the maximum weight of crop being 16.1 mg. as compared with 4.7 mg. in the control. This behavior is difficult to explain. Possibly a replacement of thiazole by the excess pyrimidine has occurred. This phenomenon, although not previously observed in connection with the components of thiamin, has been noted in the case of other growth factors (see Schopfer, 1943).

Biotin has a decidedly beneficial effect but the dosage required for maximal activity is relatively large, this factor being the most active of all the vitamins. These results may be explained by the fact that a concentrate of the vitamin was used rather than the crystalline product. The progressive increase in activity with increased dosage (beyond the usual optimum) is probably caused by impurities in the preparation. The identity of these impurities is not revealed by the data. Apparently substances other than thiamin, pyridoxine and riboflavin are present since dry matter production obtained by relatively large dosages of biotin alone was far greater than that obtained by a combina-

TABLE 1.—The effect of vitamin supplements on dry matter production by *Collybia velutipes*. The figures represent the weight in mg. (mean of 8 replicates) plus and minus the standard error. Growth period, 21 days.

Vitamins added	Dosages of vitamins in gammas per 26 ml. of medium								
	Control	0.0001	0.001	0.01	0.1	0.5	1.0	10.0	100.0
B_1	4.6±0.9	9.2±1.2	10.5±0.6	12.3±0.8	16.9±0.4	19.6±0.6	20.9±0.7	22.4±0.5	21.9±1.1
T	4.3±0.7	7.5±0.9	8.9±1.1	13.6±1.1	15.5±0.8	19.7±1.2	21.4±1.0	21.6±0.7	23.2±1.3
P	4.7±0.7	4.7±1.0	6.8±0.9	9.8±1.2	14.5±1.1	14.9±1.4	15.9±0.6	15.5±0.8	16.1±1.1
T*+P*	4.2±0.6	6.4±0.8	7.8±1.1	10.0±1.1	16.1±1.0	20.7±2.2	21.7±1.6	20.2±1.5	22.1±1.3
B	5.6±0.9	7.9±1.0	8.7±1.2	10.1±1.1	12.3±0.8	21.5±1.2	24.2±1.5	46.4±2.3	.....
B_6	6.7±0.5	8.7±0.7	8.2±0.9	7.6±1.5	8.9±1.3	8.8±1.4	9.6±0.8	9.0±0.6	8.9±1.3
B_2	6.9±0.3	7.8±0.6	8.2±1.0	8.0±1.1	9.3±0.7	7.3±0.9	8.2±1.4	9.1±0.3	9.3±1.6
B_6, 10γ + B_2**	5.8±0.8	7.5±1.1	6.3±0.9	8.5±1.2	6.8±0.8	6.2±0.8	8.2±1.4	7.8±1.3	8.1±0.6
B_6, 10γ + B	5.7±0.6	5.2±0.9	5.1±0.7	6.4±1.2	13.7±1.3	25.9±1.9	34.5±2.3	54.8±2.8	.....
B_2, 10γ + B	4.2±1.0	4.1±1.2	6.9±1.1	6.9±0.9	12.5±1.6	15.3±1.9	32.6±2.4	55.5±3.1	.....
B_6, 10γ + B_2, 10γ + B	5.2±0.9	5.7±0.8	6.8±0.8	8.4±1.1	12.0±1.4	15.6±1.4	30.4±2.1	52.2±3.2	.....
B_6, 10γ + B_1	6.0±0.6	8.4±1.0	9.9±0.7	10.9±0.9	16.8±1.2	18.7±0.9	24.5±1.3	23.6±1.5	22.3±2.0
B_2, 10γ + B_1	5.8±0.6	7.9±1.2	9.8±0.7	10.2±0.8	17.8±1.4	18.5±1.2	19.9±1.1	22.3±1.5	19.6±1.0
B, 0.1γ + B_1	12.9±1.0	15.4±0.9	16.1±1.3	16.3±0.8	17.2±0.7	19.7±1.9	20.0±0.6	22.8±1.5	21.7±2.0
B_6, 10γ + B_2, 10γ + B, 0.1γ + B_1	12.8±0.5	13.0±0.6	13.7±0.8	14.3±1.1	15.9±1.4	20.1±1.3	19.9±1.8	22.5±0.9	20.0±2.3

Key: B_1=Thiamin, T=Thiazole, P=Pyrimidine, B=Biotin, B_6=Pyridoxine, B_2=Riboflavin.

* Each of the thiamin components was supplied in equal dosage as indicated by the figures at the head of the columns.

** When two or more vitamins were supplied, the dosage of all but one was held constant; the one furnished in varying amounts appears last in the lists in the left hand column.

TABLE 2.—The effect of various supplements added to a basal medium on dry matter production by *Collybia velutipes*. The figures represent the weight in mg. (mean of 8 replicates) plus and minus the standard error. Growth period, 21 days.

Supplements	Dosages of supplements in mg. per 26 ml. of medium							
	Control	0.01	0.1	0.5	5.0	50.0	100.0	500.0
Yeast extract	6.3±0.7	17.0±2.0	23.8±1.2	27.8±1.8	31.6±1.6	68.3±3.2	113.2±5.2	385.2±14.0
Malt extract	6.8±0.8	15.2±1.5	16.8±1.7	21.7±2.0	38.7±1.8	76.6±2.8	96.6±5.1	193.4±9.2
Bacto-peptone	5.3±1.2	5.7±0.8	5.8±1.0	5.5±0.7	12.1±1.4	98.6±4.5	113.9±5.3	91.0±4.8
Bacto-agar	5.1±0.7	5.0±1.1	5.7±0.6	4.8±0.8	6.2±1.2	27.3±2.1	35.4±2.4	149.2±7.3
Glycine	6.3±1.2	.....	.....	7.8±0.6	8.5±0.7	9.1±1.3	9.3±1.2	8.4±1.7
Thiamin, 10γ + glycine	6.2±0.4	.....	.....	19.9±1.4	20.5±1.7	24.7±1.0	23.6±1.5	22.7±1.2

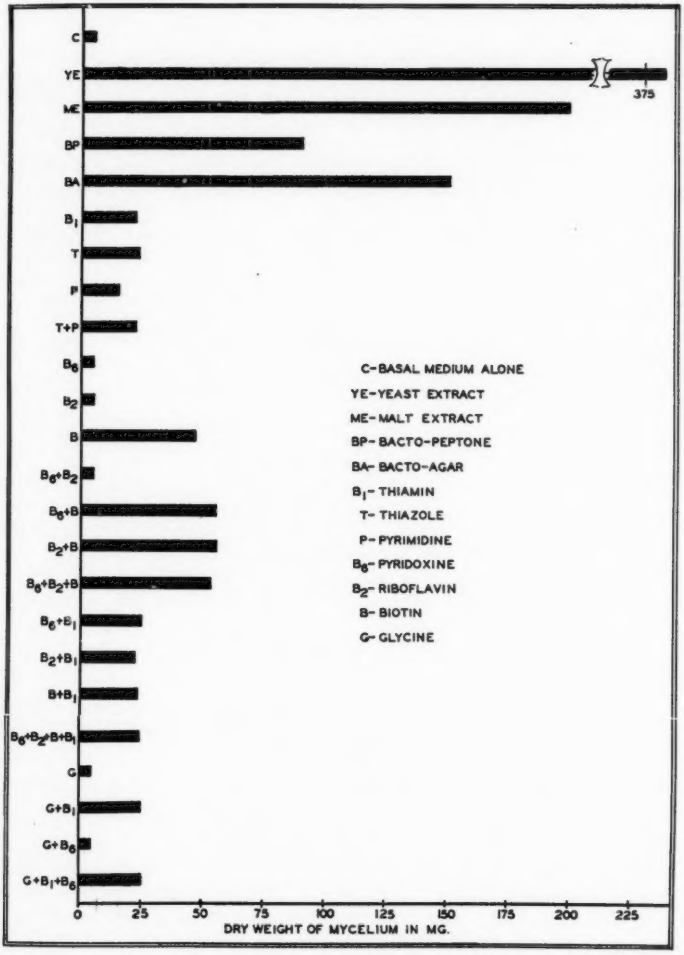

Fig. 1. Growth of *Collybia velutipes* on a basal medium with and without supplements.

tion of these three vitamins. The biotin sample undoubtedly contains other impurities.

Pyridoxine and riboflavin have no effect on the growth of *C. velutipes* either when employed alone, together, or in various combinations with biotin and thiamin. The increase in the production of dry matter resulting from the use of each of these two substances in conjunction with biotin could probably be ascribed to the activity of biotin alone.

The vitamin requirements of *C. velutipes* are not limited to thiamin (or its components) and biotin. This conclusion is supported by the fact that the combination of these two vitamins is not nearly as effective as are supplements prepared from natural products such as yeast extract, malt extract, and Bacto-peptone. These materials are effective in such small amounts that their primary action appears to be largely a function of their vitamin content. The results obtained through the addition of these products are presented in Table 2 and Fig. 1.

Yeast extract is active in dosages as low as 0.01 mg. per 26 ml. of medium, the increase in dry matter production being nearly 300 per cent. A dosage of 5.0 mg. has somewhat greater activity than an optimal dosage of thiamin. This amount of yeast extract is rather small and its effect in this dosage is probably due largely to the action of vitamins rather than ordinary nutrients. It seems likely, therefore, that yeast extract supplies, in addition to thiamin, other vitamins or highly active substances required by *C. velutipes*. Moreover yeast extract may act by supplying traces of mineral elements (concerning the action of mineral elements see Steinberg, 1936). This aspect of the problem, however, was not investigated. When the dosage of yeast extract is increased until relatively large, dry matter production continues to advance far beyond that obtained with vitamin preparations. In this case the action of the yeast extract is probably in the main that of ordinary nutrients such as nitrogen. The influence of readily available nitrogen on the growth of fungi has been pointed out by Schopfer (1943).

Malt extract has about the same activity as yeast extract when used in dosages of 50 mg. per 26 ml. of medium but, when supplied in dosages of 500 mg., its activity is only half as great. Apparently the difference in activity at the higher dosage levels is dependent on the ordinary nutrient materials.

Bacto-peptone is active only when supplied in relatively large dosage (above 5 mg. per 26 ml. of medium). This fact may be considered as an indication of the low thiamin content of peptone (Noecker, 1938). The rapid increase in dry matter production with increased dosage of Bacto-peptone at the higher level may then be regarded as a function of thiamin acting in conjunction with assimilable nitrogen.

Bacto-agar has no activity in dosages of 5 mg./26 ml. medium but above this dosage level a significant increase in growth is evident. These data indicate that this product contains thiamin and/or other factors favorable to the growth of *C. velutipes*. The presence of traces of thiamin or its intermediates in Difco-

agar has been reported by Robbins (1939) and in Difco as well as Eimer and Amend brands of agar by Day (1942). Another possible action of agar is indicated by Ripple (1936) who observed that very small amounts (0.1 per cent) of agar were highly effective in promoting the growth of *Azotobacter* and *Aspergillus*. He concluded that the effect was purely physical since various extracts were inactive. In the case of *C. velutipes*, this type of action seems possible since small dosages (50 mg./26 ml. of medium—0.2 percent) brought about a 500 per cent increase in dry matter production by this fungus. The difficulty in obtaining reliable data on dry matter production in the presence of agar is recognized by the author. However, the figures are indicative, because the cultures which yielded the greater dry weights were also the more luxuriant in appearance.

The results obtained through the use of crude products such as yeast exract and Bacto-peptone suggested the possible action of assimilable nitrogen. For this reason an attempt was made to identify the more favorable nitrogen sources of *C. velutipes*. Schopfer (1943) demonstrated that large amounts of readily available nitrogen stimulate growth in fungi thereby interfering with vitamin studies. Because White (1937) found that glycine can replace a mixture of nine of the more complex amino acids in the culture of excised tomato roots, the importance of this amino acid in the nitrogen nutrition of *C. velutipes* was investigated. It was supplied in various concentrations to the basal medium and was used alone and in combination with thiamin, but in all cases proved to be inactive. The dry matter produced by glycine plus thiamin is no greater than that produced by thiamin alone. These findings were not at all surprising in view of the fact that *Trichophyton interdigitale* requires several amino acids according to the work of Mosher, Saunders, Kingery, and Williams (1936). They found that leucine is almost indispensable, that aspartic acid and alpha-amino-beta-hydroxy-n-butyric acid are very helpful, and that a varied assortment of amino acids is more active than any combination of three or four. Similar observations were made by Woolley and Hutchings (1940) concerning two species of hemolytic streptococci which require at least seven amino acids. Woolley and Hutchings arrived at this conclusion on the basis of experiments, in which they omitted one of 19 amino acids at a time. This type of study should be applied to *C. velutipes*.

In conclusion, it may be said that *C. velutipes* requires thiamin, and one or more unidentified factors contained in yeast and malt extract. This fungus also responds favorably to other substances, possibly amino acids, present in natural products such as peptone, and extracts of malt and yeast.

Summary

1. The agaricaceous fungus *Collybia velutipes* (Curt.) Quél. was investigated concerning its vitamin nutrition.

2. The addition of thiamin to the basal medium brings about a 400 per cent increase in dry matter production. The thiazole component is as effective as the whole molecule of thiamin indicating that pyrimidine is synthesized.

The pyrimidine component is also active but its action is not as great as that of thiazole. The explanation of this behavior is not clear.

3. Biotin (a concentrate) is only slightly active when supplied in a relatively small dosage (0.1 gamma/26 ml. of medium) but is highly effective when supplied in a relatively large dosage (5 gammas/26 ml. of medium).

4. Pyridoxine and riboflavin are ineffective when supplied singly, together, or in conjunction with thiamin and/or biotin.

5. Yeast and malt extract are more active in small amounts (5 mgs./26 ml. of medium) than is a combination of thiamin, biotin, pyridoxine and riboflavin. This result indicates the presence in the extracts of a factor or factors other than the vitamins investigated.

6. The results obtained through the use of relatively large dosages of crude products such as yeast extract, malt extract, and Bacto-peptone suggest the action of assimilable nitrogen. The identity of the active nitrogenous substances was not ascertained.

7. Small amounts of Bacto-agar result in an increase in the production of dry matter, possibly through its physical rather than chemical properties.

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Observations on the Vitamin Requirements of Stereum frustulosum (Pers.) Fr.[1]

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In a previous publication the senior author (1938) reported that *Stereum frustulosum* requires thiamin as an accessory growth substance. The present paper concerns further studies on the vitamin nutrition of this fungus. This investigation deals with the optimal dosage of thiamin, the action of the thiamin components (pyrimidine and thiazole), and the effects of the vitamins riboflavin, pyridoxine, and biotin. In addition, the effect of yeast extract and that of small amounts of agar was studied.

The procedure and the basal medium employed in this investigation were essentially the same as those used by Fries (1938) in his extensive studies on the nutrition of wood destroying fungi. The ingredients of the medium were as follows: ammonium tartrate, M/10; sucrose, M/5; potassium phosphate, M/20; magnesium sulphate, M/100; ferric chloride, trace; distilled water was used to obtain the desired dilutions. The basal medium was used alone and with various vitamins or vitamin containing supplements. The culture medium was dispensed in 125 ml. Erlenmeyer flasks at the rate of 25 ml. per flask, sterilized in an autoclave, cooled and inoculated by mycelial transfer through the use of small (2 mm. x 2 mm.) hyphae-containing agar cylinders cut from the margin of inoculum cultures grown in Petri dishes. The experimental cultures were then incubated for four weeks at 25°C, collected on weighed filters, and the dry weights of the cultures were then determined in accordance with the usual gravimetric procedure. The production of dry matter was used as the criterion for the response to the vitamin supplements. The mean weight for each series of ten replicates was determined and the probable error was then calculated according to the directions given by Sherman (1941). The significance of differences between various means was ascertained by calculating the ratio between the difference between means and the probable error of the difference. The difference between two means was considered highly significant when the above ratio equaled or exceeded 3.5. This value means that the chances are 100:1 that the difference between the means is a real one and not one due to sampling error.

The mean dry weights of the cultures together with the probable errors are presented in Table 1. The ratios of the differences between certain means divided by the probable error of the difference are presented in Table 2.

The data in these tables show that thiamin brings about a significant increase in dry matter production (compare series 1 and 3 in Table 1). The difference between the two means is four times greater than the probable error of the difference, and the chances are therefore 142 to 1 that the observed dif-

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ference is a real one and not attributable to sampling error. The optimal dosage of thiamin is approximately 0.1 gamma per 25 ml. of medium. Further increase in the dosage of this vitamin is without significant effect (compare series 3 and 4 in Table 1; also see line four of Table 2).

Experiments concerning the activity of the thiamin components showed thiazole to be as effective as the entire molecule of thiamin. Pyrimidine, on the other hand, does not increase dry matter production; in fact, this vitamin appears to have an inhibiting effect. This type of action has not heretofore been observed with pyrimidine and should be reinvestigated.

TABLE 1.—The effect of various vitamin supplements on dry matter production by *Stereum frustulosum*. The figures in the column for dry weight represent in each case the mean of ten replicates. The dosage of the various supplements is given in gammas per 25 ml. of medium by the numbers occurring in parentheses.

Series No.	Supplements	Dry wt. mg.		Probable error
(1)	None—basal medium alone (Control)	13.1	±	0.47
(2)	Thiamin (0.05)	15.5	±	1.99
(3)	Thiamin (0.1)	18.4	±	1.23
(4)	Thiamin (0.5)	23.2	±	2.61
(5)	Thiamin (1.0)	20.3	±	1.89
(6)	Thiazole (0.5)	23.8	±	1.62
(7)	Pyrimidine (0.5)	10.0	±	0.56
(8)	Thiazole (0.5) + Pyrimidine (0.5)	20.4	±	1.79
(9)	Thiamin (1.0) + Pyridoxine (25.0)	19.7	±	1.23
(10)	Thiamin (1.0) + Riboflavin (12.5)	24.6	±	1.28
(11)	Thiamin (1.0) + Biotin (0.1)	22.9	±	1.52
(12)	Thiam. (1.0) + Pyrid. (25.0) + Ribo. (12.5)	19.9	±	1.09
(13)	Thiam. (1.0) + Pyrid. (25.0) + Bio. (0.1)	19.2	±	1.26
(14)	Thiam. (1.0) + Ribo. (12.5) + Bio. (0.1)	18.1	±	1.79
(15)	Thiam. (1.0) + Ribo. (12.5) + Bio. (0.1) + Pyrid. (25.0)	19.3	±	3.56
(16)	Yeast extract (1,000)	27.4	±	1.97
(17)	Yeast extract (10,000)	25.5	±	1.26
(18)	Agar, 0.1 per cent, + Yeast extract (1,000)	31.0	±	1.67
(19)	Agar, 0.1 percent, + Yeast extract (10,000)	51.0	±	1.69

TABLE 2.—The ratios of the differences between various means and the probable error of the differences. The larger of the means appears at the left. The dosage of the various supplements is given in gammas per 25 ml. of medium by the numbers occurring in parentheses.

Thiamin (0.05) — Control	1.1
Thiamin (0.1) — Control	4.0
Thiamin (0.5) — Control	3.8
Thiamin (0.5) — Thiamin (0.1)	1.7
Thiazole (0.5) — Control	7.8
Thiazole (0.5) — Thiamin (0.1)	2.6
Control — Pyrimidine (0.5)	4.2
Thiazole (0.5) + Pyrimidine (0.5) — Control	3.9
Thiamin (1.0) —Thiazole (0.5) + Pyrimidine (0.5)	0.9
Thiazole (0.5) — Thiazole (0.5) + Pyrimidine (0.5)	1.4
Thiam. (1.0) + Ribo. (12.5) + Bio. (0.1) + Pyrid. (25.0) — Control	1.7
Thiam. (1.0) — Thiam. (1.0) + Ribo. (12.5) + Bio. (0.1) + Pyrid. (25.0)	0.3
Yeast extract (1,000) — Thiamin (1.0)	3.9
Yeast extract (1,000) — Yeast extract (10,000)	0.8
Agar, 0.1 per cent,+ Yeast extract (1,000)—Yeast extract (1,000)	1.0
Agar, 0.1 per cent,+ Yeast extract (10,000) — Yeast extract (10,000)	12.7

The combination thiazole plus pyrimidine has about the same activity as thiamin. This response is according to expectations based on the fact that thiazole is as active as the entire molecule of thiamin.

The vitamins riboflavin, pyridoxine, and biotin are inactive with respect to dry matter production by *S. frustulosum*. A combination of these three vitamins together with thiamin is no more effective than thiamin alone. The series of cultures receiving the above combination of four vitamin supplements was superior to the series growing on the unsupplemented basal medium but the difference was not statistically significant. This lack of significance is perhaps due to the great variation in the cultures growing on the vitamin supplemented medium.

Yeast extract which is known to be an excellent source of at least eight B vitamins was employed as a supplement to the basal medium. The results indicate that this product contains factors other than thiamin favoring the growth of *S. frustulosum* (compare series 5, with series 16 in Table 1). The optimal concentration of yeast extract is 1,000 gammas per 25 ml. of medium. Further additions of this extract are ineffective. This optimum is relatively low indicating that the effect of yeast is, in the main, due to the vitamins supplied by it.

Observations of cultures growing on liquid and solid media indicated that the agar used in the solid media had a beneficial effect. The nature of the effect may be multiple. Agar contains growth factors (Robbins, 1939 and Day, 1942) as well as mineral elements which are likely to interfere in nutrition studies (*cf.* Schopfer, 1943). Furthermore, agar has been shown to exert a strictly physico-chemical effect on organisms (Rippel, 1936). In an attempt to determine the nature of the effect of agar on *S. frustulosum*, small amounts of washed[2] agar were added to the culture medium. The agar was supplied at the rate of 0.1 per cent and was used in conjunction with yeast extract at two dosage levels, namely, 1,000 and 10,000 gammas per 25 ml. of medium. At both levels beneficial effects were demonstrated by the appearance of the cultures and also by the dry matter produced. However, the increase in dry matter production was statistically significant only when the agar was accompanied by the 10,000 gamma dosage of yeast extract. Apparently an ample supply of the factors found in yeast extract must be present in the culture medium for the maximal action of the agar. The effect which washed agar exerts on *S. frustulosum* is very similar to that observed by Rippel on *Aspergillus*. These organisms when cultured on a liquid medium in the absence of agar remain confined near the margin and the surface of the culture medium. When a small amount (as little as 0.1 per cent) of agar is supplied, the culture forms a uniform mat over the surface of the medium. The action of the agar, therefore, appears to be strictly physico-chemical in nature.

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2 The washed agar was prepared according to directions given by Fred and Waksman (1928).

Summary

1. *Stereum frustulosum* was investigated concerning its vitamin nutrition.

2. Thiamin, riboflavin, pyridoxine and biotin were tested but only thiamin proved to be beneficial to this organism. This vitamin is as effective as yeast extract. The optimal dosage of thiamin is 0.5 gamma per 25 ml. of culture medium.

3. Thiazole is as effective as the whole molecule of thiamin. Apparently the other component of thiamin (pyrimidine) is synthesized by the organism.

4. Small amounts of washed agar exert a beneficial effect on *S. frustulosum*. This action is probably strictly physico-chemical in nature.

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The Mating Types of Double Animals in *Euplotes patella*[1]

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The mating types in *Euplotes patella* and the genetic mechanism determining them were described almost concurrently with the morphology and cytology of the double animal of this species (see citations to Kimball below). The double animal contains two nuclear complexes, one or both of which can be involved in conjugation with single animals of various mating types. Since these two nuclear complexes occur together in the same cytoplasm while retaining their individualities, this question arose: what would be the mating type of a double animal containing two nuclear complexes each of which determined a different mating type? This paper presents the evidence concerning this question, a summary of which has appeared previously (Powers, 1942).

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Material and Methods

The organism used was that variety of *Euplotes patella* which has been analyzed by Kimball (1939a, 1941b, 1942) for mating types. All the stocks used in this work are descendants of the ones referred to by him, and they were cultured in the manner described by him.

The mating types and their genetic basis in *Euplotes patella* have been described by Kimball (1939a, 1942b). There are six mating types numbered I through VI. Ordinarily no conjugation is observed in an unmixed culture; but when a culture is mixed with one belonging to any one of the five other mating types, conjugation occurs. Kimball postulates that the six mating types are determined by a system of multiple alleles having three members. These three alleles—designated mt,[1] mt,[2] mt,[3]—can exist in the nuclei of the animals in all possible paired combinations, the six types being assigned these genotypes: type I, mt^1 mt^2; type II, mt^1 mt^3; type III mt^3 mt^3; type IV mt^1 mt^1; type V, mt^2 mt^3; type VI, mt^2 mt^2.

The double animal, the experimental animal in this work, was also described by Kimball (1941a). It consists of two single animals fused together along their right aboral sides. Each half is so oriented in relation to the other half that the double is a homopolar, symmetrical animal whose two oral regions

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are completely free of each other. The original double arose as a result of an incomplete division of a single animal, followed by a twisting of the two components until their right aboral sides were fused along their entire length. This animal possessed a macronucleus and a micronucleus in each half, and it divided vegetatively at right angles to the antero-posterior axis. During division the macronucleus and the micronucleus in each half behaved as they do in singles during division, and the cytoplasmic organelles in each half were fully reformed. It was possible, therefore, to obtain large numbers of these animals similar to the parental one. Some of the descendants, however, lacked one of the micronuclei. Since these unimicronucleate doubles were just as viable as the bimicronucleate ones, they were used to begin new lines, and it was from such a line that the double animals used by the author were obtained.

The double animals conjugate in appropriate mixtures both with other double animals and with single animals. Kimball (1941a) described the variety of conjugant groups that are formed under certain conditions. Single-single pairs, double-double pairs, single-double pairs, and single-double-single combinations are among the most frequent types of associations observed in mixtures of double animals with the proper kind of singles. Unimicronucleate, as well as bimicronucleate, double animals conjugate with singles in these manners, and this fact was taken advantage of in obtaining the double animals of desired genetic constitutions. If, for instance, a double animal having the constitution of type IV on one side and type III on the other was desired, double animals containing but one micronucleus of type IV were mixed with single animals of type III. The single-double pairs formed were isolated, and then the exconjugant doubles showing two macronuclear anlagen were kept as the desired type. The explanation is as follows: if the single conjugates with the micronucleate half of the double, there is an exchange of pronuclei between the two and the formation of a syncaryon in each one. In the double this syncaryon gives rise to a single macronuclear anlage and a micronucleus with the genotype possessed by type II animals. If, however, the single animal conjugates with the amicronucleate half of the double (see Fig. 1) the single animal provides one pronucleus which enters the amicronucleate half of the double and which subsequently gives rise to a micronucleus and a macronuclear anlage. At the same time, the micronucleus on the other side of the double gives rise to two pronuclei which probably unite in autogamy, and this autogamous syncaryon gives rise to a micronucleus and a macronuclear anlage. The exconjugant double from this type of association, then, will evidence two macronuclear anlagen, one of these being derived from a syncaryon containing only mt^1 genes and the other being derived from a hemicaryon containing only an mt^3 gene or genes. It can be seen, therefore, that the genotype of the exconjugant double animal can be predicted within limits if the following information is known: the genotype of the single animal involved; the number of micronuclei in the double involved as well as the genotypes of these micronuclei; the type of association between the single and the double in conjugation; and the number of macronuclear anlagen in the exconjugant double animal. All the double animals used in this investigation were obtained in such a manner.

To ascertain precisely the genotypes of the double animals advantage was taken of the fact that at times a double animal at division gives rise to two single animals and a double instead of two double animals. Double animals occasionally become widely separated at the anterior end. The plane of division then may pass through the wings of the Y, thus producing two complete singles and a double. Isolation of one of these widely separated doubles and recovery of the two singles produced after the subsequent division was the standard technique. These two singles were cultured separately and tested for mating type; and since each mating type is determined by a different genotype, this gave precise knowledge of the genotypes of the nuclear complexes in the double.

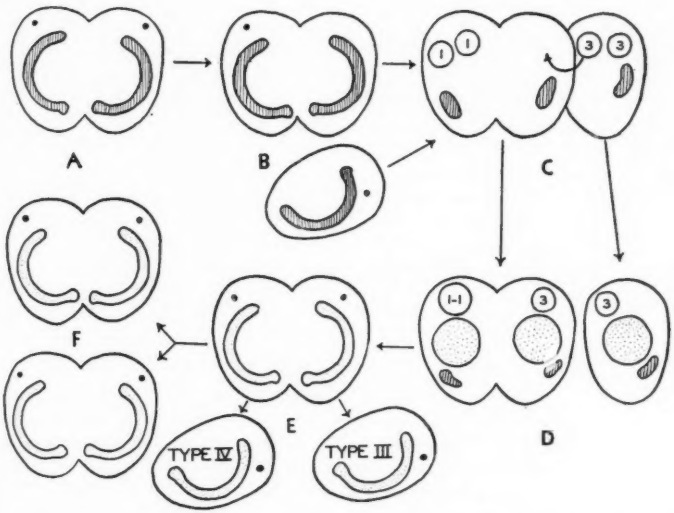

Fig. 1. Diagrams representing the method of breeding double animals of desired genotypes. A double animal (A) loses one of its micronuclei, retaining one containing the gene *mt*1. This animal mates (B) with a single of type III. If the single mates with the amicronucleate half of the double, the single will provide (C) the double with a pronucleus containing the *mt*3 allele, and the two pronuclei produced in the micronucleate half of the double will fuse. When these two animals separate, the double contains (D) two macronuclear anlagen and two micronuclei—one homozygous for the *mt*1 gene and the other presumably hemizygous for the *mt*3 gene. This double reorganizes completely, and from it there can be obtained eventually a single (E) from each half of the double, one of which will test as type IV and the other of which will test as type III. The double also produces (F) many doubles like itself and these are used to test the mating type of the double with it nuclear components intact within the common cytoplasm. In the figures the cross-hatched structures are the preconjugation macronuclei; these usually disintegrate during conjugation. The circular stippled structures are macronuclear anlagen which arise from the syncaryon or the hemicaryon as the case may be, and which give rise directly to the new macronuclei.

The tests for the mating types of the singles obtained above were carried out in accordance with the standards set up by Kimball (1942). A line was considered to be of the same mating type as a standard line if these conditions were fulfilled: no mating in a mixture between the two lines; the occurrence of a definite mating reaction in mixtures of the tested line with the other five standard lines; and a mating reaction between the sixth standard line and one other. The last condition is necessary because some instances of a lack of reaction have their bases probably in the unfavorable physiological condition of the lines involved (Kimball, 1942) rather than in the lines' possessing a similar mating type. In all instances controls consisting of unmixed animals of each of the lines used were set up at the time of mixture. If any of these unmixed animals was observed in conjugation, the tests involving the line were discarded. The same criteria were used in testing the double animals, but one more precaution had to be taken. Because of the production of single animals by the doubles, these singles had to be removed before the test singles were introduced in order that only one type of single animal be present.

In contrast to the situation in various species of *Paramecium* (Sonneborn, 1939; Jennings, 1939; Gilman, 1942), the pairs formed in *Euplotes patella* do not always consist of animals belonging to lines of different mating type. Kimball (1941a) showed this by mixing singles and doubles of different mating types—almost all conceivable types of association were observed. In these experiments, then, a mating reaction was adjudged to be one consisting of a certain minimum number of pairs or larger groups, regardless of the type of their association. Forty pairs were arbitrarily set as the minimum because the irregular mating which occasionally occurred rarely equalled this number.

The Continuity of the Cytoplasm between the Halves of a Double Animal

In his description of the double animals, Kimball (1941a) presents evidence which makes it fairly certain that no membrane exists which separates the halves of the organism. First, the manner of formation of the doubles, having its beginning in the incomplete cytoplasmic division in a dividing single and proceeding by an increase in the area of fusion between the two singles, leads one to such a conclusion. Further, observations made on an elongated single macronuclear anlage formed in some doubles stretching from one half into the other constitute proof of cytoplasmic continuity between the two halves. To make this conclusion completely certain, however, it was deemed desirable to examine sections of the double animals.

Figure 2 is a transverse section of a double animal cut just anterior to the mouth. The animals were fixed in Schaudinn's fluid, sectioned at approximately 5 micra, and stained with Mallory's triple stain. The figure plainly shows that the pellicles of the two halves are continuous with each other and that there is no indication of a separating membrane or pellicle between the two halves. This observation supports those mentioned above in proving that the double animal is effectively a single mass of cytoplasm with two nuclear complexes.

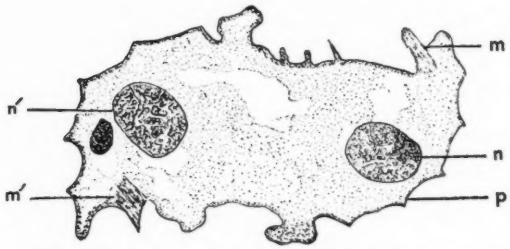

Fig. 2. A sketch drawn with the aid of a camera lucida of a transverse section of a double animal in *Euplotes patella*. The section is just anterior to the mouth on either side. The letters denote the following: m, m′ = membranelles bordering the oral grooves; n, n′ = macronuclei, one in each half of the animal; p = pellicle. (×880, approx.).

The Mating Types of Double Animals Containing Known Mating Type Genes

In order to study the effect of two nuclear complexes of different genotype on the mating type of the double animal, three steps had to be taken. First, double animals with the desired combinations of mating type genes had to be obtained through appropriate matings. Second, it had to be ascertained that the genotypes of the nuclear complexes were actually those desired by obtaining a single from each half of the double and testing for mating type the lines raised from these. Finally, the double animals themselves had to be tested for mating type.

Table 1 is a summary of the results obtained. The results are classified into nine different sorts or kinds based upon the genotypic constitutions of the doubles and the mating types exhibited by the doubles. The information presented under "Nuclear constitution of double" is based finally upon the results of testing for mating type each of the two lines of single animals which originated after "splitting" the double into its component singles. Each of these groups of singles exhibited only one mating type and since each mating type is determined by only one kind or by a particular combination of two of the three mating type alleles, the genotypes of the doubles could be written as soon as the tests were complete. The term "(IV+VI)," then, means that the double in question yielded two lines of singles—one of type IV mating type and the other of type VI. The expression "$(mt^1mt^1 + mt^2mt^2)$" denotes only the *kinds* of mating type alleles present in each nuclear complex. It is important to note that even though two alleles are written to describe each nuclear complex, the thesis that all the nuclei possess the same number of genes is not advanced. Some of the homozygous (hemizygous, perhaps) nuclear complexes arose from single pronuclei, and at least the micronuclei of these complexes should have but half the number of chromosomes found in some other micronuclei. This matter is discussed more fully in a later section of the paper.

The column "Number of lines tested" includes in each instance all the lines of doubles of that kind which have been fully tested. Each of these lines originated at conjugation independently of all others—vegetatively each is unrelated to any other, whether of the same constitution or of different constitutions.

The results of sort 1 show that the mating type of a double animal containing only mt^1 genes in one nuclear complex and only mt^2 genes in another nuclear complex in the same cytoplasm is the same as that of a single animal containing these two different genes in a single nuclear complex, i.e., type I. Five other lines of double animals were tested completely and they reacted with all mating type singles except those of type I. These, shown in results of

TABLE 1.—A summary of the mating types of double animals of various genotypes. The designation "(IV + VI)" indicates that this double animal possesses two nuclear complexes, one of which determines in the single animal the type IV mating type and the other of which determines the type VI. The expression "$(mt1mt1 + mt2mt2)$" is the genic restatement of the nuclear condition of the double. In these genic expressions the number of genes of any kind which is written is not necessarily to be considered the true state of affairs—only the kinds of genes written are significant. The nuclear constitution of the doubles of sort 6 as well as the unexpected difference between the results of 8 and 9 are discussed in the text.

Sort of result	Nuclear constitution of double	Number of lines tested	Mating type of double	Genotype of single of similar mating type
1	(IV + VI) $(mt1mt1 + mt2mt2)$	4	I	$mt1mt2$
2	(I + VI) $(mt1mt2 + mt2mt2)$	5	I	$mt1mt2$
3	(III + IV) $(mt3mt3 + mt1mt1)$	4	II	$mt1mt3$
4	(II + III) $(mt1mt3 + mt3mt3)$	2	II	$mt1mt3$
5	(III + V) $(mt3mt3 + mt2mt3)$	1	V	$mt2mt3$
6	(? + ?)	4	V	$mt2mt3$
7	(III + III) $(mt3mt3 + mt3mt3)$	1	Reacted with types I, IV and VI only	None
8	(IV + IV) $(mt1mt1 + mt1mt1)$	1	Reacted with types III, V and VI only	None
9	(IV + IV) $(mt1mt1 + mt1mt1)$	1	Reacted with types I, III, V and VI	None

sort 2, were found to be heterozygous for the alleles mt^1 and mt^2 in one nuclear complex, and to have only the mt^2 allele in the other. These two kinds of results show that the mating type of the double is determined by the kinds of alleles present, their position in regard to the nuclear complexes in the double having no observable effect. Mating type I is determined whenever the two genes mt^1 and mt^2 are present, whether they occur together in the same nuclear complex (as in a single animal) or whether they are separated into different nuclear complexes (as in the double animals above).

Some of the type VI nuclear complexes in double animals of sort 2 (as will be shown later) arose from single pronuclei at conjugation. The micronuclei, if not the macronuclei, in these are expected to contain but one half the number of chromosomes found in the heterozygous micronuclei. There is, then, present in this kind of double at least twice the number of mt^2 genes as there are mt^1 genes. Yet, no differences were observed between the mating reactions of these and those of any other line. It might be said, therefore, that no dosage effect of the genes is observable.

The same general result is observed when the genes mt^1 and mt^3 are present together in the double. The results of sort 3 parallel those of sort 1, and those of sort 4 parallel those of sort 2. Mating type II, which is determined in the single when these two genes are together in the same nuclear complex, is determined also in the double even though each of the two genes involved is located in a different nuclear complex. From the results mentioned thus far, therefore, we see that the three mating type alleles in *Euplotes patella* are expressed whenever they are present in the animal.

There remains to be considered one other heterozygous combination of the known mating type genes. No complete results are at hand on a double animal of type V which is homozygous (or hemizygous) in each half for the mating type genes present in each half. Unfortunately, the lines of doubles reported in the results of sort 6 and the singles derived from them were lost before the tests on the singles were completed; therefore, the genotypic constitutions of the nuclei present are not directly known. The evidence from their origins, however, taken together with their mating types, indicate that they were pure for the mt^2 gene in one half and for the mt^3 gene in the other. All four arose from a mixture of a unimicronucleate line of double animals with type III singles. Each of the doubles was associated with but one single during conjugation, and each of the exconjugants double animals possessed two macronuclear anlagen. The preconjugant double, according to its origin, could have possessed only an mt^1 gene, or an mt^2 gene, or both, in its micronucleus. The single, then, was the only source of the mt^3 allele, and its pronucleus must have entered the amicronucleate side of the double during conjugation to produce a complex pure for mt^3. (See Fig. 1, which is a similar instance.) If the conclusions concerning the activity during conjugation of the micronucleus in an unmated side of a double are correct, the micronucleus in these doubles must have undergone autogamy, and the resultant nuclear complex was pure for either the mt^1 gene or the mt^2 gene. The fact that the double lines produced by this mating were of mating type V indicates that the mt^2 gene

must have persisted in each of the four instances. These four lines, then, were probably pure for the mt^2 allele on one side and for the mt^3 on the other. The group, therefore, demonstrates for the mt^2-mt^3 combination the same kind of activity seen in the mt^1-mt^2 and the mt^1-mt^3 combinations. The results of sort 5 bear the same relation to those of 6 as those of 2 bear to those of 1, and those of 4 bear to those of 3.

The results obtained after mixing singles of the six mating types with doubles containing but one kind of gene for mating type were different from those presented above. In Table 1 these results are presented as sorts 7, 8 and 9. In sort 7 a double line containing in either nuclear complex no mating type allele other than mt^3 failed to react with or induce a reaction in singles of types II, III, and V. There were no pairs observed at any time in mixtures of these animals with singles of type III, and the number of pairs seen in mixtures of the doubles with types II and V at no time exceeded ten. This low reactivity is in strong contrast to the pairing seen in mixtures of this line of doubles with the other three kinds of singles (in one instance over one hundred single-single pairs were observed). It might be pointed out here that the types with which this double line failed to exhibit mating reactions are types which are determined in part by the allele present in this double line—type II being determined by mt^1mt^3 and type V being determined by mt^2mt^3.

That this kind of result is not peculiar to the mt^3 allele is demonstrated by the results of sort 8. This line of doubles possessed mating type alleles of only the mt^1 kind, and in mixtures of this line of doubles with singles of types I, II and IV, no mating reactions were observed. The mixtures were repeated at least six times during a period of a month and a half. No pairs were ever formed in mixtures with type IV singles; there was occasional pairing of mixtures with type II, but the highest number of pairs seen at any one time was three (all double-double pairs); and the highest number of pairs seen in mixtures with type I singles was one (also a double-double pair), except in one instance when approximately sixty pairs of singles were observed. In this last instance, however, the control for the type I standard used contained at least forty pairs, indicating a strong "selfing" propensity on the part of this line at the time. This test may be disregarded, therefore, at this time. The results obtained with this line of doubles agree with those observed with the pure type III double. Here, the double containing mating type alleles of only the mt^1 kind failed to react with or regularly induce reactions in singles of the genotypes mt^1mt^2, mt^1mt^3, and mt^1mt^1. It is to be noted that each of the singles contains the mt^1 gene, the one for which the double is pure.

According to the results obtained above with the two homozygous lines of doubles, it may be expected that no mating reactions involving singles will occur when the homozygous doubles are mixed with singles containing a mating type gene in common with them. Yet the results observed after testing the line of doubles reported in the results of sort 9 are not consistent with this expectation. This line of doubles undoubtedly was pure for mt^1 in both its nuclear complexes. Yet, according to the laboratory records mixtures of this line with

singles of types I, III, V, and VI showed definite, clear-cut mating reactions. Although there was mating observed also in the mixture with the singles of type II, the fact that there was pairing in the unmixed control of these singles makes this reaction a less positive one. It will be shown below in the next section that the fact that there was pairing observed in the type I mixture is in itself not surprising nor unexplainable—but the fact that there were many single-single pairs does not constitute an unexplainable aberration. It will be shown that the kind of mating that is expected in these instances above where no or very little mating was observed is that kind which involves only the double animals. Observations have indicated that pairing involving doubles are not nearly so frequent as those involving singles alone. Therefore, it is not surprising that very few or no conjugant groups were found in the mixtures in which the doubles alone were expected to conjugate. However, the unexpected pairings of singles in the mixture of doubles of sort 9 with type I singles are not readily explainable with any information at hand.

In summary it can be said that double animals containing at least two of the three kinds of mating type alleles exhibit a definite mating type in that they do not mate with or fail to induce mating in singles of one of the six mating types, and that this mating type is the one characteristic of a single containing these two alleles in its single nuclear complex. This phenomenon is exhibited by the doubles whether the two genes involved are located in the same nuclear complex in the double, or are separated into different nuclear complexes in the same cytoplasm. Double animals containing but one kind of gene fail to induce conjugation regularly in singles which contain a mating type allele in common with them.

Types of Associations Formed in Single-double Mixtures

On the basis of Kimball's (1942) observations on the importance of the nature of the fluid in relation to conjugation in *Euplotes*, one does not expect that in a mixture of any two different mating types there always should be formed pairs between the animals of different mating type. Indeed, the evidence from the single animals indicates that in certain mixtures at times, in contrast to the situation described in the various species of *Paramecium*, only one of the two kinds of organisms present conjugates at all. By mixing fluids, in which one type of animal had grown, with animals of other types Kimball has shown that the following generalization usually holds: animals of any one mating type are not induced to conjugate unless the foreign fluid to which they are exposed was obtained from animals containing a mating type allele different from the ones present in the animal used for mixture. Thus, fluid from type I animals (mt^1 mt^2) induces conjugation of type IV animals (mt^1 mt^1), but the reverse mixture does not result in conjugation. Type III fluid (mt^3mt^3) induces type IV animals to conjugate, and the reverse mixture also results in conjugation. In the experiments reported here, single animals are mixed with double animals; and since each kind is usually recognizable, animals of each mating type are marked. To test the generalization as stated by Kimball, an attempt was made, therefore, to note the kinds of associations

observed as well as their frequencies in mixtures of the doubles with the different kinds of singles.

Table 2 is a summary of the observations. These data were gathered during the testing of the mating types of the various kinds of doubles and they represent observations taken from many different lines and cultures at different times. The results from double animals possessing similar genotypes in regard to mating type are grouped together; and these are added to those

TABLE 2.—Numbers of conjugant associations involving at least one double animal found in mixtures of the indicated kinds of double animals with singles of the standard mating types.

Genotypes of doubles*	Number of lines tested	Standard mating types and their genotypes					
		I	II	III	IV	V	VI
		$mt^1\,mt^2$	$mt^1\,mt^3$	$mt^3\,mt^3$	$mt^1\,mt^1$	$mt^2\,mt^3$	$mt^2\,mt^2$
$mt^1mt^1 + mt^2mt^2$	4	0	85	87	11	99	7
$mt^1mt^2 + mt^2mt^2$	5	7	156	65	13	248	40
Sum	9	7	241	152	24	347	47
$mt^1mt^1 + mt^3mt^3$	4	82	0	5	1	39	53
$mt^1mt^3 + mt^3mt^3$	2	87	0	0	4	101	78
Sum	6	169	0	5	5	140	131
$mt^2mt^3 + mt^3mt^3$	1	67	42	0	12	0	0
$mt^1mt^1 + mt^1mt^1$	1	22	4	89	0	33	26
$mt^1mt^1 + mt^1mt^1$	1	3	5	50	0	10	22

* The nuclei in all instances here are represented as diploid ones; this is not necessarily true for nuclei containing but one kind of gene.

from double animals showing a similar phenotype, even though the genes involved are arranged differently in the nuclear complexes. The results reported earlier, which show that kinds of alleles present in the double and not their position in regard to the two nuclear complexes regulate the mating behavior of the double, justify such combinations of results here.

Examination of the table reveals that the conclusions of Kimball concerning which animals conjugate when two kinds are mixed are partially but not wholly supported. For instance, when doubles of constitution (IV + VI) or (I + VI) are mixed with singles of all the types, we expect according to the theory presented above that these doubles will be induced to conjugate only when they are put into fluid produced by animals containing the mt^3 allele. Therefore, we expect to find conjugation involving these doubles in mixtures with singles of mating types II, III and V. The table very clearly shows that the doubles of this constitution conjugated much more frequently when mixed with these three kinds of singles than they did when mixed with the singles of types I, IV, and VI. The fact that these doubles conjugated when mixed with types, IV and VI, even though on a very much smaller scale, constitutes an exception which is discussed below.

Similarly, doubles containing the alleles mt^1 *and* mt^3 are expected to conjugate only when in fluid produced by singles containing an mt^2 gene. There

are three mating types which contain the mt^2 allele, and the table shows that when mixed with singles of these three types (I, IV, and VI) the doubles conjugated very frequently in comparison to the amount observed with the other three kinds of singles. In the case of doubles possessing alleles mt^2 and mt^3, we expect no doubles to be involved in conjugation when mixed with singles of types III, V, and VI—these being the three types which do not contain the mt^1 allele. The one line of doubles of this kind whose genotype is definitely known fulfills the expectations clearly.

In the case of double animals containing but one kind of mating type allele, there were two kinds of results obtained: one line evidenced results of the type discussed above; the other evidenced results which were of a slightly different kind in that conjugation of doubles was present in apparently significant numbers when the line was mixed with four of the types of singles. Because of this fact, the two lines in question, even though they possess the same genotype, $[(mt^1mt^1 + mt^1mt^1)]$, are listed in the table separately.

Theoretically, a homozygous double line should be induced to conjugate when mixed with five of the six kinds of singles. It contains but one kind of gene, and should, therefore, be affected by the two kinds of substances produced when the two other kinds of mating type alleles are present, at least one of which is present in each of the five mating types different from the one to which the double belongs. In Table 2 it can be seen that the double line reported on next to the last line (sort 9 in Table 1) almost fulfills the expectation. The lack of conjugation of the doubles when mixed with singles of type II is, if the theory concerning the immediate causes of conjugation is correct, the unexpected feature. One other unexpected fact not shown on the table is that many single-single pairs were observed in all the mixtures except that with the type IV singles. The single-single pairs in the mixtures with singles lacking the mt^1 allele are consistent with the theory concerning conjugation, but those in the mixtures with types I and II are not.

The double line of the same constitution reported on the last line of Table 2 showed a significant number of conjugating doubles only when mixed with three of the six kinds of singles. This is one of the double lines which were described in the preceding section concerning the lack of reaction observed in certain mixtures of homozygous double lines. Not only did the double animals fail to conjugate in these mixtures but the singles did not conjugate either. The failure of the singles to conjugate is evidence which supports the general theory; the failure of the doubles to conjugate does not destroy the theory. As stated above, doubles apparently do not conjugate as readily as singles. It is conceivable that in this instance the conjugation-inducing substances were not sufficiently powerful to induce conjugation of the doubles in mixtures with singles of types I and II.

Although the observations reported here support in general Kimball's (1942) theory concerning conjugation, several exceptions have been noted. These exceptions are of two kinds: first, a lack of conjugation where it should occur; and second, the presence of conjugating animals of a particular kind

where they, according to the theory, are not expected. The first kind of exception may be explained by assuming unfavorable physiological conditions at the time of mixture as suggested above. The second type of exception indicates either that the theory is incorrect, or else that there are unknown factors which regulate conjugation in addition to those described by him. It has been stated above that conjugation does occur occasionally in unmixed samples, and Kimball (1942) has indicated the occurrence of unexpected matings. It seems permissible to assume that as yet unrecognized controlling factors operate at the time of conjugation; and the need for further investigation of this phenomenon is patent.

Mating Types of Unimicronucleate Double Animals

The problem of whether the micronucleus or macronucleus or both are involved in mating type determination in *Euplotes* has not been satisfactorily answered. Evidence concerning this question was obtained from a series of experiments designed to test the effects of the loss of a micronucleus from a double animal. The result of this loss, if it had any effect, could have been of great importance in this work. In order to demonstrate that the unimicronucleate animals in these cultures were of the same mating type as the original bimicronucleate ones, and that, therefore, a test on a mixed culture gives an accurate indication of the phenotype of the line, the following experiments were performed.

A series of isolations were made of double animals from line K1921a. These isolated animals were allowed to divide several times, and then several animals from each depression were stained and examined for micronuclear number. Most of these contained two micronuclei, but some had only one. The animals which were sisters of the stained animals containing but one micronucleus were saved. Since K1921a was one of the four lines of sort 1 in Table 1, one micronucleus and one macronucleus of this line were genotypically type IV, and those in the other half were genotypically type VI. This procedure, then, resulted in cultures of animals each of which contained one micronucleus—genotypically either type IV or type VI—and two macronuclei, one derived from a type IV syncaryon and the other derived from a type VI syncaryon (hemicaryon, perhaps). Since all the animals of any one culture are vegetative descendants of one isolated animal, all in each culture presumably are alike.

Complete tests against standard singles were made on four such cultures. All reacted as type I animals, the type expected if the two kinds of alleles known to be present in the original bimicronucleate double line are active. Since either the micronucleus containing the mt^1 alleles, or else the one containing the mt^2 alleles, is absent, the determining influence cannot be said to have arisen from the micronucleus in these instances.

It is probable that these results were not due to the persistence of the effect of the lost micronucleus comparable to the "lag effect" reported by Kimball (1939b) for the mating types in *Paramecium aurelia*. The isolations were

made in early October, and the tests for mating were made in the following December and January. This means that at least two months, representing about 30 to 40 vegetative fissions, elapsed between the loss of the micronucleus and the time of testing. Further, if the micronucleus is the important active agent during vegetative life as far as mating is concerned, it is difficult to understand why the remaining micronucleus had not imposed its type on the whole double animal, i.e., the double animal should have reacted either as type IV or as type VI, not as type I. The micronucleus, then, by these experiments seems to be eliminated as the *sole* determining agent. It cannot be said, however, that the micronucleus does not play some part in mating type determination, for the evidence of Kimball (1941a) indicates that the micronucleus has very important vegetative functions. Amicronucleate lines rarely survive four divisions and, when they do survive for a longer period, possess low vigor throughout their short lives.

Since the above evidence indicates that the micronucleus is not the only determining agent in producing mating type, (if it has any effect at all in regard to the active determination of mating type during vegetative life), mating type must be determined by one of two other agents,—the cytoplasm and the macronucleus—or both together. Undoubtedly the genetic agents must act through the cytoplasm, and in this sense the cytoplasm can be said to be active in the determination. But the fact that the double animals can be "split" into two singles of different mating types, each of which may be different from the original double animal in regard to mating type, indicates that the cytoplasm is not "fixed" for mating type, and that the determining influences must come from another source. There remains, then, only the macronucleus as the proved determiner of mating type in *Euplotes patella*.

This organism is, therefore, like *Paramecium aurelia* and *P. bursaria* in this regard. In the former organism, Sonneborn (summarized, 1942b) demonstrated that the macronucleus must be the controlling agent in the production of the mating type of the individual: two animals, the products of the division of one, differ in mating type only when the division separates two independently formed macronuclei; amicronuleate races of organisms always possess definite mating type; and organisms which possess macronuclei which result from the regeneration of parts of old macronuclei always belong to that mating type characteristic of the old nuclear complex. To account for the fact that two macronuclear anlagen derived from a single syncaryon can differ in genotype, Sonneborn (1942a) assumes a high mutation rate at the time of the production of the macronuclear anlagen—thus implying that there are genetic determiners which are acting directly from the macronucleus. Jennings (1939) bases his conclusions concerning this question in *P. bursaria* on observations on the mating types of the animals gained after the post-conjugation division at which the new macronuclear anlagen are separated.

Although the general conclusion concerning the determination of mating type by the macronucleus is similar in the three species of ciliates, the details are not equally clear in all cases. Sonneborn (1940) states that the macro-

nucleus in *Paramecium aurelia* "must contain at least 40 complete and discrete genomes." The evidence for this statement is based upon observations on the characters of animals possessing macronuclei which represented regenerated fragments of old disintegrated macronuclei. Such a statement cannot be made concerning *Euplotes patella* or *P. bursaria* with the evidence at hand. Indeed, Turner's (1930) observation that in *E. patella* part of the old macronucleus is often incorporated in the new post-conjugation macronucleus, taken together with the fact that exconjugant animals usually belong to the types expected from the matings, indicates that at conjugation the macronucleus of *E. patella* loses its old genetic character. Of course, it must be admitted that definite conclusions concerning this cannot be drawn until a precise study of the effects of the persistence of parts of the old macronucleus into the new post-conjugant animal has been made.

Therefore, it can be said that the macronucleus in *Euplotes patella* determines the mating type of the individual organism which is inherited by way of the pronuclei produced by the micronucleus or micronuclei, but the question as to whether the macronucleus contains genetic determiners similar to those in the micronucleus is still open.

Observations on the Genetics of the Doubles

In the section concerning the methods which were used in this investigation a description was given of the method of obtaining double animals of desired genotypes by appropriate mating of certain kinds of doubles with certain kinds of singles. It was implied that the method did result in lines of double animals which were desired. It is of interest to point out directly, however, what certain of the results of these matings were, since they support Kimball's (1941a) statements concerning the nuclear events in a conjugating double.

Two of the lines reported in the results of sort 1 in Table 1 arose from conjugant pairs consisting of a double and a single. The parental doubles were unimicronucleate animals belonging to mating type IV (mt^1mt^1) and the parental singles were of mating type VI (mt^2mt^2). Since the double exconjugant in each instance possessed two macronuclear anlagen, the prediction was made that the double animal gained the genome of one of its halves from the single parent and the genome of the other of its halves from the double parent. In other words, the double enconjugant should have been of mating type VI in one half and of mating type IV in the other. These two lines of doubles were "split" into their component singles, and the tests for mating type of the single lines obtained revealed that one of the lines did belong to mating type IV and the other belonged to mating type VI in each instance. Three of the lines reported in the results of sort 2 in Table 1 were obtained from the same mixture of the singles of type VI with the doubles of type IV. These double lines, however, arose from exconjugants which when conjugating were associated with two single animals, one on each side. In each instance a pronucleus from the single animal should have entered each side of the double; and, therefore, each nuclear complex of the double should have contained the

mt^2 allele. Since the double contained in one side mt^1 genes the resultant exconjugant double in every case should have had the genotype ($mt^1mt^2 + mt^2mt^2$). In the three instances the "split" test showed that the double animal contained one nuclear complex determining mating type I and one other determining mating type VI.

Examination of the histories of eight of the other double lines reported in Table 1 shows that they exhibited the genotypes expected according to the explanation offered by Kimball of the genetic mechanisms determining mating type in *Euplotes patella* and of the cytological processes occurring in the double during conjugation. The lines included those which were shown to contain the following genic associations: ($mt^1mt^1 + mt^1mt^1$); ($mt^1mt^1 + mt^2mt^2$); ($mt^1mt^1 + mt^3mt^3$); ($mt^1mt^3 + mt^3mt^3$); and ($mt^2mt^3 + mt^3mt^3$). It can be seen that every one of the three alleles for mating type is involved. These results support fully Kimball's explanation of the behavior of the nuclei in the double during conjugation, as well as providing supporting proof of the described genetic relationships existing among the mating types. They also strengthen the theory concerning the genotypes of the double animals of sort 6 in Table 1 discussed on page 181.

One of the (IV + VI) double lines whose origin was described above was mixed with a single line of type VI. Double lines were obtained from three single-double-single associations. In each instance the exconjugant double contained two macronuclear anlagen. According to the expectation, these doubles should, if the preconjugant double possessed two micronuclei, have been (I + VI); or, if the preconjugant double in each instance possessed but one micronucleus, the exconjugant line should have been (VI + VI) or (I + VI). Two of the three double lines fulfilled this expectation—they tested as (I + VI) animals. These two lines are included in the results of sort 2 in Table 1. One of the double lines did not fulfill this expectation—it was shown to have the constitution ($mt^1mt^1 + mt^2mt^2$). Apparently, the pronucleus from the single animal associated with the type IV half of the double either failed to enter the double; or, it did not contain elements that could actively determine mating type; or else, one of the single animals was a type IV animal produced by the double line itself. This last possibility cannot be eliminated in spite of the care taken to remove all singles from cultures of doubles before mixture with other singles.

One other instance of this kind was noted. A double animal from a line of sort 3 in Table 1, (III + IV), was associated with one single of type VI during conjugation. The exconjugant double contained two macronuclear anlagen, and it was expected, therefore, that the mt^2 allele would have been in evidence in the new double line. The doubles evidenced, however, the same constitution as the parental double, (III + IV). This constitution is expected only if both sides of the double underwent autogamy, or if the pronucleus which entered the double from the single did not contain an active mt^2 allele, or if the single animal was a type III or type IV animal produced by the doubles and not an introduced type VI single at all.

If the pronuclei in these two instances did not pass into the doubles concerned, the two constitute examples of "cytogamy." This phenomenon was described by Wichterman (1940) in *Paramecium caudatum*, and in *P. aurelia* by Sonneborn (1942b).

There were two other lines of doubles whose origins could be explained only by hypotheses different from those above. One exconjugant double contained two macronuclear anlagen after having been associated with one single during conjugation. The preconjugative constitution of the double was (III + IV) and the single was type VI. Contrary to all expectations, whether they are based upon the presence of one or of two micronuclei in the double, the new double line was shown to be (IV + IV). The "split" test in this instance fortunately can be confirmed by the fact that mixtures of these homozygous doubles with singles of types I, II, and IV evidenced very weak mating reactions or none at all. In another instance a unimicronucleate double which could have had the constitution only of (I + 0), or (IV + 0), or (VI + 0) was associated with a single of type III. The exconjugant double showed two macronuclear anlagen, and the double line arising from it was (III + III). This unexpected combination of nuclear complexes is confirmed by the very weak mating reactions observed in mixtures of these doubles with singles of types II, III, and V.

The first of these double lines could have arisen conceivably as a result of the mating of a type IV single (produced by the double line) which was not removed from the culture before the type VI singles were introduced. If the type III half of the double was amicronucleate and the type IV single mated with this side, a double would be expected with the constitution (IV + IV) as observed. This kind of explanation, however, is not valid for the origin of the second line of doubles. Since the mt^3 allele could have been contributed to the exconjugant doubles only by the introduced singles, the exconjugant double line must have gained its mating type from these singles alone. To account for the presence of the mt^3 gene alone in each half of the double it seems most logical to assume that the type III single contributed a pronucleus to the double during conjugation, and that this pronucleus underwent the normal post-conjugation nuclear processes without fusing with a pronucleus furnished by the double. It is conceivable that after the formation of the four post-conjugation nuclei the usual disintegration of two of these did not occur; instead, they persisted, resulting in the production of two nuclear complexes determining type III.

One other fact was learned from an examination of the histories of the double lines. In seven of these lines the genotypes could have been obtained only if the single animal in each instance contributed to the double a pronucleus which did not fuse with another pronucleus in the double. In other words, the genetical picture allows only that some of the nuclear complexes arose from "hemicarya." It is evident from what has been said before that these hemicarya do give rise to nuclear complexes. In the double animals these nuclear complexes determine mating type as actively as those derived from

syncarya. Hemicaryon formation was described first in *Paramecium bursaria* (Chen, 1940), and cytological evidence of it in *Euplotes patella* was presented by Kimball (1941a). The seven lines noted here constitute the first demonstration of normal genetic activity, as far as mating type is concerned, of nuclear complexes derived from single pronuclei.

Discussion

The proof that each of the two nuclear complexes in a double animal is active in the determination of the mating type of the double gives information concerning the nature of the action of the determining alleles which supports the conclusions of Kimball (1942). He gives evidence for the existence of three conjugation-inducing substances in the fluid in which the animals are grown, each substance being produced when a certain one of the three alleles determining mating type is present. Animals are induced to conjugate when in the presence of substances which they themselves do not produce. These data explain why fewer pairs on the average are found in mixtures of animals of a heterozygous mating type with animals homozygous for one of the alleles in the heterozygote. These facts lead him to believe that the heterozygote may be considered "a simple combination of two homozygous phenotypes" and that the genes are acting independently of one another. It has been shown here that the heterozygous mating types are determined even when the genes concerned are separated into different nuclear complexes; each allele is contributing to the heterozygosity of the phenotype and the same result is produced as that observed when the two alleles are present in the single nuclear complex possessed by the single animals. Apparently, each gene affects the cytoplasm independently. Kimball's explanation of the immediate cause of conjugation in terms of substances produced by the animal allows us to understand how this condition can obtain—each gene is responsible in some manner for the production of a certain kind of substance, and this substance retains its individuality regardless of what other kinds are present. The alleles, then, are said to act in an independent manner.

This particular kind of evidence (*demonstrably active* genetic determiners located in different nuclei which in turn are located in the same cytoplasmic mass) concerning the activity of genes in animals has not been presented as far as the writer knows. There are, however, some instances in plants. Clark (1940, 1942) has shown that normal microsporic development in *Zea Mays*, although dependent upon the presence of a full haploid complement (McClintock, 1938), is not dependent upon the complement's localization into a single nucleus. Similar to this is the evidence of Sax (1942) who observed normal growth in microspores in *Tradescantia* containing incomplete genomes provided the spores were attached to others that were complete or complementary. He suggests that there is a diffusion of "gene products." In some of the fungi where nuclei contributed by the parental lines commonly remain separate until late in vegetative life pertinent data are to be found. Hansen and Smith (1932) indicate that the heterotypes of the imperfect fungus *Botrytis cinerea* are explained by heterocaryosis—the presence of

different kinds of haploid nuclei in the cytoplasm of the organism. Burgeff's (1912) production of neutral mycelia in *Phycomyces* by the fusion of (+) and (–) hyphae and his (1914) observations on the *piloboloides* variant of *P. blakesleeanus* possibly are two examples of the desired type of evidence. Kniep (1929) agrees that in these two instances there are probably at least two types of nuclei present.

The Ustilaginales, investigated extensively genetically, furnish several examples of internuclear actions in the determination of genetic characters. Goldschmidt (1928) showed that two lines of *Ustilago violacea*, each specialized for infecting a different host-plant, produced when crossed a dicaryotic mycelium capable of infecting either type of host. Christensen and Rodenhiser (1940) recognize the significance of Goldschmidt's observation by remarking that "associations of two haploid nuclei of different parasitic abilities may have physiologically the same effect as if they had fused to give a diploid stage." Also, Christensen (1929) observed that different dicaryons in *Ustilago zeae* obtained from crosses of various strains were not equally virulent: certain dicaryons infected the host more successfully than others. A similar type of results is recorded by Hanna (1929) who investigated the same organism. The report of Allison (1937) on the pathogenicity of *Ustilago medians*, *U. hordei*, and hybrids between the two also consists of evidence of this sort. More recently Dodge (1942) and Malloch (1942) reported results in *Neurospora tetrasperma* which demonstrate genetic determinations from two kinds of nuclei in the same cytoplasm. Dicaryosis in general is summarized by Buller, 1941. In addition to these instances, the genetic incompatibilities existing within species of flowering plants (Stout, 1938) may possibly be regarded demonstrations of inter-nuclear actions.

Apparently in many of the instances the presence of two haploid nuclei in the cell has the same effect that would result if the two nuclei had fused into a regular diploid nucleus. This fact indicates that the actions of many of the genes are not dependent upon the genes' position in regard to other genes on other chromosomes at least. The evidence from the fungi is important in this regard; but that concerning microsporic development in Zea and Tradescantia may be a little more important, not only because a multinucleate condition is abnormal in these organisms but also because a haploid complement in each instance is separated into many nuclei. It has been established that a complete genome is necessary for the development of the microspores, and in these instances, then, each of the nuclei contains necessary elements. Each nucleus, therefore, must be actively affecting the developing microspore. We may say that the effective action of a genome is not dependent upon all the genes' being enclosed in the same nucleus.

The fact that genetic determiners seem to act normally regardless of their position in some plants and in at least one animal indicates that such action may be widespread. Probably the reason why it is not recognized in animals and plants as a general rule is that the peculiar nuclear conditions necessary for its recognition are rather infrequent. However, certain characters in animals

are of such a nature that they appear to be determined by genes capable of being expressed regardless of their position in the cell. For example, the blood groups in man as well as the antigenic characteristics of the blood in birds (see Irwin and Cumley, 1943), undoubtedly involving independent alleles, probably fit into this category.

It is not difficult to understand why separation of the mating type alleles in Euplotes into different nuclear complexes has no apparent effect on the expression of either allele. Each of the three alleles apparently controls the production of a substance qualitatively different from those substances whose productions are controlled by the other two alleles. The cytoplasm of an animal belonging to a heterozygous mating type, containing a mixture of two independent substances, would be expected to be the same whether the two substances originated from one or from two nuclear complexes. It is impossible to explain the situations in the other organisms in such terms at the present time, but it is not unreasonable to believe that similar explanations will be valid for the activities of many genes. It may be suggested that even such intergenic and interchromosomal relations as epistasis, modification and suppression will still hold after the separation of the interacting elements into different nuclei in the same cytoplasm has been accomplished. Perhaps, only the true "position effects" are expressions of genic dependence upon relative position in the nucleus.

Summary

1. An investigation of the mating types of double animals in *Euplotes patella* was carried out. These double animals contain two nuclear complexes; and since the doubles conjugate with singles, doubles of various genotypes for mating types were obtained.

2. Stained sections of double animals revealed no separating membrane or pellicle between the component halves; the cytoplasm in the double is continuous.

3. Double animals containing two nuclear complexes, each of which is pure for a different mating type gene, belong to the mating type determined in the single by the same two alleles occurring together in the same nuclear complex. Separation of the two genes concerned, then, is seen to have no effect on the mating type determined by any combination of two mating type alleles. Two of the three possible kinds of doubles of this sort were investigated fully, and incomplete evidence concerning the third kind is given.

4. Double animals heterozygous for two mating type alleles in one nuclear complex and pure for one of these alleles in the other complex belong to the mating type characteristic of singles containing these two kinds of genes in their single nuclear complexes. The mating reactions of these organisms indicate no dosage effects of the mating type genes. The three possible kinds of doubles of this class were investigated fully.

5. Double animals completely pure for one mating type gene reacted in a

manner different from doubles containing two kinds of alleles. The mating behavior of these doubles is discussed in detail.

6. The types of associations formed in mixtures of singles and doubles are summarized and analyzed. The conclusion is reached that the analysis supports partially, but not fully, the theory describing the immediate causative factors governing mating in a mixture of animals of two different mating types. Several exceptions noted suggest that there are factors, at times causing conjugation, which are not included in the theory based upon the study of the conjugation-inducing power of the fluids.

7. The mating type of a unimicronucleate line of doubles arising from an originally bimicronucleate line is the same as the original line in the four groups of this kind tested. Since any effect of the lost micronucleus is eliminated by the number of vegetative fissions intervening between the time of loss and the time of testing, it is concluded that the micronucleus is not the only agent determining mating type in *Euplotes patella*. The cytoplasm is shown not to be "determined," and the conclusion is drawn that mating type in this organism is under the control of the macronucleus.

8. The ancestries of 15 lines of doubles, whose genotypes include the three kinds of mating type alleles, support the general theory of the genetic determination of mating type offered by Kimball. They constitute also confirmation of his descriptions of the cytological processes occurring in double animals during conjugation. The histories of four lines which are exceptional are discussed.

9. According to the histories of the lines, one of the two nuclear complexes in each of seven different lines of doubles must have arisen from a hemicaryon. Since these doubles yielded normal singles from both sides, it is concluded that single pronuclei generally give rise to normally functional nuclear complexes.

10. The relation between the results of this investigation and the theory of the independent action of the mating type alleles is discussed briefly. Evidence, gained from other organisms, of the type presented in this paper is reviewed, and the bearing of all the evidence on genic expression in general is briefly discussed.

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Studies on Monogenetic Trematodes—

X. Gill Parasites from Reelfoot Lake Fishes*

John D. Mizelle and John P. Cronin

Introduction

Reelfoot Lake, from which the specimens of fish parasites were taken for this work, was formed about the time (1811) that the first venturesome pioneers began to settle along the banks of the Mississippi River. The Chickasaw Indians who dwelt near the great river had a chief called Kalopin or Reelfoot because he had a deformed foot and walked with a rolling motion. The Indian legend concerning the formation of Reelfoot Lake relates that Reelfoot while seeking the hand of the daughter of a great Choctaw chief, Copiah, sought to steal her when he was refused and thus incurred the wrath of her father and the Great Spirit. The Great Spirit spoke to Reelfoot admonishingly and told him that to steal a wife from a neighboring tribe was against tribal law and that the penalty for such an act was the loss of the offender's land and the burial of his people in a watery grave. Nevertheless, Reelfoot stole the princess, an earthquake occurred, and Reelfoot Lake was formed where Reelfoot's tribe had lived. "Where the Great Spirit stamped the earth, the Mississippi formed a beautiful lake, in the bottom of which lay Reelfoot, his bride, and his people" (Nelson 1924).

The pioneers who lived at New Madrid, Tennessee, also chronicled the formation of the lake. Eliza Bryan wrote that on December 16, 1811, a violent shock (earthquake) followed by several lighter shocks occurred. During the earthquake the Mississippi River overflowed its banks in waves from fifteen to twenty feet high. "Earth waves" in the area came up through two thousand feet of sand and clay, and where breaks occurred on the earth's surface, streams of quicksand produced veritable "sand geysers." Reelfoot Lake was thus formed and later became the home of many fishes and birds, being located in the most-used highway of the migratory birds (Nelson 1924).

In 1910 the State of Tennessee made Reelfoot Lake a fish and game preserve. It is fifteen miles long by five miles wide and lies approximately parallel to the Mississippi River from which it is separated by Lake County. The lake is situated in the northwest corner of the State of Tennessee next to the Kentucky boundary, has an average depth of ten feet, drains into the Mississippi River by way of a southern outlet, and is fed by three small streams on the eastern side. The vegetation in the lake consists principally of cypress trees, lily pads, seed moss, and wild rice.

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Materials and Methods

Twenty-seven vials of gill material from Reelfoot Lake fishes, collected by Dr. Venard, were examined. Involved were eight host species, namely, *Ameiurus melas* (Rafinesque), *A. natalis* (Le Sueur), *Amia calva* Linnaeus, *Ictalurus furcatus* (Le Sueur), *I. lacustris punctatus* (Rafinesque), *Huro salmoides* (Lacépède), *Lepomis microlophus* (Günther), and *L. miniatus* Jordan. All of the host material except that from *Amia calva* was infected. Descriptions of parasites from *L. miniatus* were published by Mizelle and Jaskoski (1942). The parasites from the remaining hosts are treated in the present paper. These consist of seven new, and ten described, species of Tetraonchinae.

The host material was first frozen and then preserved in five per cent formalin. The gills were placed in small vials about two-thirds full of tap water and shaken vigorously in order to free the parasites from the branchial tissue. This material was then transferred to watch glasses and diluted and decanted until clear enough for reliable examination with a binocular microscope.

Individual specimens were collected with a capillary pipette equipped with a rubber bulb and transferred to clear water for further removal of mucus. Individual specimens were transferred (one each) to a drop of solidified glycerin-gelatin medium on a clean glass slide. A cover-glass which was placed thereon settled into place as the medium was melted with gentle heat. The slide was then cooled, the medium congealed, and a permanent mount was thus produced. Four hundred slides were prepared in this manner. Of these, two hundred thirteen were selected for measurement and observation.

Measurements were made with a compound microscope and a calibrated ocular micrometer for (1) body length, (2) greatest body width, (3) length and (4) width of haptor, (5) length of bars (two), (6) length and (7) width of anchors, (8) length of cirrus, (9) length of accessory piece, (10) length of hooks, and (11) transverse diameter of pharynx. Curved structures were measured as a straight line extending between the two most distant parts of such structures. Measurements for anchor lengths, for example, extend from the tip of the superficial root of the base to the most distal point on the curved portion in the region of junction of the shaft and point. The width of the anchors is the greatest width of an anchor base measured at right angles to the anchor shaft. A mean measurement was calculated (in cases involving three or more specimens) and consists of an average derived from the measurements of the same structure in different individuals. All measurements, except those for (1) body length, (2) body width, and (3) length and (4) width of haptor which were made with a low-power (16 mm.) objective, were done with an oil-immersion objective. Measurements enclosed in quotation marks

in a given description are taken from the sources indicated. Other measurements (not so enclosed) are those obtained from the material dealt with herein.

Description of Species

Actinocleidus bakeri n. sp.

Pl. 1, Figs. 1-10

Host and Locality.—Red-Eared or Stumpknocker Sunfish *Lepomis microlophus* (Günther), Reelfoot Lake, Ridgely, Tennessee.

Specimens Studied.—Three.

Type Specimens.—Cotypes, U.S. Nat. Mus., Washington, D.C.

Description. — Moderately small dactylogyrids with a smooth cuticula. Length 0.555 mm. (0.536-0.571 mm.), greatest body width 0.069 mm. (0.064-0.071 mm.). Peduncle moderate to elongate. Haptor semilunar in outline and generally with a bulge on each side of the posterior (truncate) surface. Haptoral width 0.079 mm. (0.071-0.086 mm.), length 0.054 mm. (0.050-0.057 mm.). Haptoral bars dissimilar. Anterior bar bent posteriorly in the middle and with the two halves connected by a very thin bridge (Pl. 1, Fig. 1). Anterior bar length 0.046 mm. (0.043-0.051 mm.). Posterior bar smaller, straight to slightly bent in the middle and with a shallow notch distally on the internal surface of each arm (Pl. 1, Fig. 2). Posterior bar length 0.031 mm. (0.028-0.032 mm.). Anchors similar in size and shape, bases bifurcate, and with regularly recurved shafts and points. Anterior anchor shafts and points solid, those of posterior anchors hollow (Pl. 1, Figs. 7-10). Length of anterior anchors 0.029 mm. (0.027-0.031 mm.), width of bases 0.009 mm. (0.008-0.010 mm.). Length of posterior anchors 0.030 mm. (0.029-0.032 mm.), width of bases 0.009 mm. (0.008-0.010 mm.). Hooks fourteen in number, subequal in length and normal in arrangement. Each hook is composed of a relatively large oval solid base, a slender solid shaft, a sickle-shaped termination, and an opposable piece (Pl. 1, Fig. 4). Hook bases much shorter than the shafts. Hook lengths 0.014-0.019 mm. Eye spots four, members of anterior pair smaller and closer together or farther apart than members of posterior pair. Cephalic lobes vestigial or absent, pharynx subcircular in dorsal outline, transverse diameter 0.025 mm. (0.024-0.028 mm.). Gonads situated near middle of body; ovary ovate in outline, comparatively small, diagonally or longitudinally elongate; testis ovate to elliptical in outine, longitudinally elongate, larger than, and situated immediately posterior to, the ovary. Vagina chitinized, sinistral, and located in the anterior half of the body (Pl. 1, Fig. 3). Seminal receptacle not observed. Copulatory complex consisting of an attenuate cirrus and a knobbed accessory piece (Pl. 1, Figs. 6, 5 resp.). Cirrus with a comparatively large base, curved shaft, and pointed extremity; cirrus length 0.023 mm. (0.021-0.026 mm.). Accessory piece with a raised portion (knob) near the midlength. Accessory piece length 0.017 mm. (0.016-0.018 mm.). Vitellaria moderately developed and extend to the peduncle.

The closest relative of this species is difficult to determine. The accessory piece is similar to that of *Actinocleidus gracilis* Mueller, 1937, *A. fergusoni* Mizelle, 1938(a), and others, while the cirrus is different from that of any other species in the genus. The anchors have bifurcate bases which are remotely similar to those in *A. fusiformis* (Mueller, 1934) and the anterior anchors are solid (posterior pair hollow) as in this species (*A. fusiformis*, Mizelle, 1940, Figs. 1, 2). The anterior bar is remotely similar to that of *A. harquebus* n. sp. but is singular in that the middle portion is very narrow and forms a connecting bridge between the two halves. Articulating surfaces on the anterior bar are vestigial whereas those of the posterior bar are well developed but apparently not separate from the bar proper (Pl. 1, Figs. 1, 2).

This species is named in honor of Dr. C. L. Baker, Director of the Reelfoot Lake Biological Station.

Actinocleidus bifidus n. sp.

Pl. 1, Figs. 11-27

Host and Locality.—Red-Eared or Stumpknocker Sunfish *Lepomis microlophus* (Günther), Reelfoot Lake, Ridgely, Tennessee.

Specimens Studied.—Eleven.

Type Specimens.—Cotypes, U.S. Nat. Mus., Washington, D.C.

Description. — Moderately small dactylogyrids with a smooth cuticula. Length 0.455 mm. (0.299-0.621 mm.), greatest body width 0.056 mm. (0.049-0.071 mm.). Peduncle short to extremely (infrequently) long. Haptor subcircular to ovate in dorsal view, width 0.067 mm. (0.057-0.093 mm.), length 0.061 mm. (0.049-0.071 mm.). Haptoral bars dissimilar and articulated with each other (Pl. 1, Figs. 11-15). Anterior bar bent posteriorly in the midportion and with a subterminal notch on the posterior border near each end, length 0.042 mm. (0.022-0.049 mm.). Posterior bar shorter, 0.025 mm. (0.020-0.031 mm.) long, and variable in shape (Pl. 1, Figs. 13-15). Both bars provided with well-developed articulating surfaces. Anchors somewhat similar in shape, and with regularly recurved hollow shafts and points. Tip of each anchor point sharply curved toward the shaft (Pl. 1, Figs. 24, 25). Anterior anchor bases bifurcate (Pl. 1, Fig. 24). Anterior anchor length 0.035 mm. (0.024-0.040 mm.), width of bases 0.010 mm. (0.008-0.011 mm.). Deep root of each posterior anchor base vestigial and appearing as a small elevation (Pl. 1, Fig. 25). Posterior anchor length 0.039 mm. (0.029-0.040 mm.), width of bases 0.010 mm. (0.009-0.011 mm.). Hooks fourteen in number, subequal in length and apparently normal in arrangement (Mizelle 1938a). Hooks of pair number five situated toward lateral surface of the haptor at end of a line drawn from a point between the two bars. Each hook is composed of a solid base, a slender solid shaft, a sickle-shaped termination, and an opposable piece (Pl. 1, Figs. 26, 27). A structure which arises from the convex surface of the sickle-shaped termination is present on each of the hooks and

probably serves as an attachment for muscles which operate the hooks. The hook bases are ovoid to elliptical (hooks of pair number one) in outline and comparatively short in relation to their respective shafts. Hook lengths 0.012-0.015 mm. Eye spots four, fragile, and composed of melanistic granules which separate readily on application of pressure. Members of the posterior pair three to four times larger, situated closer together than those of anterior pair, and at times apparently confluent. Cephalic lobes poorly developed, pharynx circular to ovate in dorsal outline, transverse diameter 0.020 mm. (0.019-0.021 mm.). Gonads ovoid to elliptical in outline, subequal in size, and situated near the middle of the body. Ovary anterior to testis. Vagina variable, well chitinized, sinistral, and situated in the posterior part of the anterior body half (Pl. 1, Figs. 22, 23); seminal receptacle not observed. Copulatory complex consisting of a characteristic cirrus and accessory piece (Pl. 1, Figs. 16-21). Cirrus sigmoid, with a large base to which the accessory piece attaches and a distal portion of smaller diameter which is bifurcate terminally. Cirrus length 0.029 mm. (0.019-0.039 mm.). Accessory piece blunt distally with a triangular process arising from the shaft and directed toward the cirrus. This process may be turned so as not to be visible at times (Pl. 1, Fig. 21). Accessory piece length 0.020 mm. (0.014-0.036 mm.). Vitellaria well developed and terminate near the peduncle.

The closest relatives of this species are *A. maculatus* Mueller, 1937 and *A. bifurcatus* Mizelle, 1941. It resembles *A. maculatus* principally in the nature of the anchors, bars, and hooks (Mueller 1937, Figs. H 29-31 and Mizelle, 1941, Figs. 17-20, 23, 24). The cirrus somewhat resembles that of *A. bifurcatus* Mizelle, 1941 (Figs. 46, 47) but the accessory piece (Pl. 1, Figs. 19, 20, 21) is decidedly different from that of any other species in the genus.

Actinocleidus crescentis n. sp.

Pl. 1, Figs. 47-54

Host and Locality.—Red-Eared or Stumpknocker Sunfish *Lepomis microlophus* (Günther), Reelfoot Lake, Ridgely, Tennessee.

Specimens Studied.—One.

Type Specimens.—Type, U.S. Nat. Mus., Washington, D.C.

Description. — Moderately small dactylogyrids with a smooth cuticula. Length 0.364 mm., greatest body width 0.046 mm. Peduncle narrow and of moderate length. Haptor discoidal in dorsal outline, width 0.046 mm., length 0.050 mm. Haptoral bars dissimilar (Pl. 1, Figs. 47, 48). Anterior bar bent posteriorly in midportion and notched near each end for articulation with anterior anchor bases, length 0.045 mm. Posterior bar with small "shoulders," articulating surfaces (with anterior bar) very large, (Pl. 1, Fig. 48), length 0.020 mm. Anchors similar in size and with regularly recurved hollow shafts and points; anterior pair larger. Anterior anchor bases bifurcate; deep root of posterior anchor bases vestigial (Pl. 1, Figs. 51, 52). Length of anterior

anchors 0.032 mm., width of bases 0.011 mm. Length of posterior anchors 0.030 mm., width of bases 0.009 mm. Hooks fourteen in number, subequal in length and normal in arrangement. Each hook is composed of an oval (in outline) solid base, a slender solid shaft, a sickle-shaped termination, and a conspicuous opposable piece (Pl. 1, Figs. 53, 64). Hook bases very short in comparison with their respective shafts. Hook lengths 0.011-0.015 mm. Eye spots four, fragile, and with members of the posterior pair larger and closer together than those of the anterior pair. Cephalic lobes of moderate size, pharynx circular in dorsal outline, transverse diameter 0.013 mm. Gonads not observed. Vagina chitinized, sinistral, and situated in the posterior part of the anterior body half; seminal receptacle not observed. Copulatory complex consisting of a terminally bifurcate cirrus and an accessory piece with a crescentic termination (Pl. 1, Figs. 49-50). Cirrus with a large base to which the accessory piece attaches; cirrus length 0.027 mm. Accessory piece with the crescentic termination attached to a lower, comparatively straight "handle" which articulates to the cirrus base. Accessory piece length 0.013 mm. Vitellaria moderately developed and extending to the peduncle.

This species is peculiar in that it possesses characteristics of two other species of the genus, namely, *Actinocleidus bifurcatus* Mizelle, 1941 from *Lepomis microlophus* (Florida) and *A. bifidus* n. sp. The cirrus of *A. crescentis* is almost identical with that of *A. bifurcatis* except that the superior termination of the former is rounded. The greatest difference in the copulatory complex of the two species under consideration is in the nature of the accessory pieces. In the present species this structure has a comparatively small base and a large crescentic termination (Pl. 1, Fig. 50) whereas the accessory piece in *A. bifurcatus* has a large base and a tapered and pointed termination (Mizelle 1941, Figs. 44, 45). The anchors, bars, and hooks of *A. crescentis* do not resemble those of *A. bifurcatus* but closely approximate those of *A. bifidus* except for certain details. *Actinocleidus bifurcatus* has been taken only from Florida *Lepomis microlophus*.

ACTINOCLEIDUS FLAGELLATUS Mizelle and Seamster, 1939

Pl. 1, Figs. 28-37

Host and Locality. — Warmouth Bass, *Chaenobryttus coronarius* (Bartram). Reelfoot Lake, Ridgely, Tennessee.

Previously Reported Host and Localities.—Warmouth Bass, *Chaenobryttus coronarius* (Bartram). Roadside Canal, Naples, Florida, and Roadside Ditch, Englewood, Florida (Mizelle and Seamster 1939).

Specimens Studied.—Eight.

Structurally the Tennessee specimens agree with those from Florida except for (1) certain differences in the anterior and posterior bars (Pl. 1, Figs. 28,, 29 and Mizelle and Seamster, 1939, Figs. 35, 36) and (2) the presence of a cuticular filament which is attached to the terminal part of the cirrus (Pl. 1, Figs. 34, 35). Average measurements for Tennessee specimens are larger than

those for Florida representatives in every instance except in the case of (1) posterior bar length, (2) anterior anchor width, and (3) cirrus length (see Table 1). Although the sample from Florida is admittedly too small to support sweeping conclusions which might be drawn, it seems striking that the maximum body length is 37 microns less than the minimum body-length measurement for Tennessee forms. In addition, the average width is greater in the Tennessee specimens than it is in the more southern representatives.

ACTINOCLEIDUS FUSIFORMIS (Mueller, 1934)

Synonyms. — *Ancyrocephalus cruciatus* (Wedl, 1858) see Cooper 1915; *Cleidodiscus fusiformis* (Mueller, 1934).

Host and Locality.—Large-Mouth Bass, *Huro salmoides* (Lacépède), Reelfoot Lake, Ridgely, Tennessee.

Previously Reported Hosts and Localities. — Small-Mouth Bass, *Micropterus dolomieu* Lacépède, State Fish Hatchery Reservoir, Constantia, New York (Mueller 1934); Ohio Hatcheries, London, Ohio, and Syracuse, New York, (Mueller 1936); and Cove Creek, Caryville, Tennessee (Mizelle 1940). Kentucky or Spotted Bass, *Micropterus punctulatus* (Rafinesque), Norris Lake, Norris, Tennessee; Cold Creek, below Norris Dam (Tenn.); and Cove Creek, Caryville, Tennessee (Mizelle 1940). Large-Mouth Bass, *Huro salmoides* (Lacépède) Peace River, Florida (Mueller 1937); Local Ponds and Streams near Stillwater, Oklahoma (Seamster 1938); New Roads, Louisiana (Summers and Bennett 1938); and Hatchery, Norris, Tennessee (Mizelle 1940).

Specimens Studied.—Five.

Measurements obtained for this species agree with those given in the redescription (Mizelle 1940) except that the minima for (1) body width, 0.060 mm. "0.068 mm.," (2) haptor width 0.064 mm. "0.082 mm.," and (3) anterior bar length, 0.039 mm. "0.049 mm." are less, and the maxima for (1) posterior bar length 0.053 mm. "0.047 mm.," (2) anterior anchor length 0.047 mm. "0.046 mm." (3) posterior anchor length, 0.054 mm. "0.053 mm.," and (4) cirrus length, 0.065 mm. "0.057 mm." are greater, than those given in the redescription. However, the specimens from the same host from Florida averaged shorter (0.483 mm.) than those from Tennessee (0.573 mm.). This species is always immediately recognizable by the anchors which possess deeply bifurcate bases, the prominent posterior bar which is generally plate-like, and the anterior bar which has bifurcate ends usually attached to the anchors between two roots of the bases. In the present specimens the cirrus was modified to the extent that the anterior part greatly resembled a large haptoral hook with a well-developed opposable piece. This modification is easily accomplished by marked development of the distal portion of the cirrus base and foreshortening of the terminal part of the cirrus. (For normal development see Mizelle 1940, Fig. 5).

Actinocleidus harquebus n. sp.

Pl. 1, Figs. 38-46

Host and Locality.—Red-Eared or Stumpknocker Sunfish *Lepomis microlophus* (Günther), Reelfoot Lake, Ridgely, Tennessee.

Specimens Studied.—One.

Type Specimen.—Type, U.S. Nat. Mus., Washington, D.C.

Description. — Moderately small dactylogyrid with a smooth cuticula. Length 0.384 mm., greatest body width 0.068 mm. Peduncle short and stout. Haptor semicircular in dorsal outline, posterior border truncate, width 0.084 mm., length 0.042 mm. Haptoral bars dissimilar (Pl. 1, Figs. 38, 39). Anterior bar bent posteriorly in midportion and modified near each end for articulation with anchor bases, length 0.051 mm. Posterior bar somewhat H-shaped and 0.030 mm. long. Both bars with well-developed articulating surfaces. Anchors similar in shape, and with regularly recurved hollow shafts (cavity very small in anterior pair) and points; posterior pair larger. Anchor bases bifurcate (Pl. 1, Figs. 43, 44). Length of anterior anchors 0.034 mm., width of bases 0.011 mm. Length of posterior anchors 0.042 mm., width of bases 0.011 mm. Length of posterior anchors 0.042 mm., width of bases 0.012 mm. Hooks fourteen in number, subequal in length and normal in arrangement. Hooks of pair number five lie ventrally near the posterior anchor bases. Each hook is composed of a solid base, a slender solid shaft, a sickle-shaped termination, and a well-developed opposable piece (Pl. 1, Figs. 45, 46). The bases are oval in outline and comparatively short in relation to their respective shafts. Hook lengths 0.029-0.034 mm. Eye spots four, fragile, and the comprising melanistic granules separate readily with pressure. Members of the posterior pair three to four times larger and much closer together than members of the anterior pair. Cephalic lobes poorly developed; pharynx ovate in dorsal outline, longitudinally elongate, and about 0.021 mm. in transverse diameter. Gonads not observed. Vagina small, sinistral, and situated in the posterior part of the anterior body half (Pl. 1, Fig. 42). Seminal receptacle not definitely observed. Copulatory complex consisting of a curved attenuate cirrus and a terminally hooked accessory piece (Pl. 1, Figs. 40, 41 resp.). Cirrus with a large base to which the accessory piece attaches; cirrus length 0.030 mm.; accessory piece with a termination similar to that of the hooks; length 0.025 mm. Vitellaria moderately developed and terminate in the body anterior to the peduncle.

A comparison of the copulatory complex of this species with that of other *Actinocleidus* species is difficult since the comprising cirrus and accessory piece are different from those in any described form. The anchors somewhat resemble those of *A. okeechobeensis* (Mizelle and Seamster, 1939, Figs. 27, 28, 31, 32). The posterior bar lacks the shoulders which are characteristic of many *Actinocleidus* species.

Actinocleidus unguis n. sp.

Pl. 1, Figs. 55-64

Host and Locality.—Large-Mouth Bass, *Huro salmoides* (Lacépède), Reelfoot Lake, Ridgely, Tennessee.

Specimens Studied.—Two.

Type Specimens.—Cotypes, U.S. Nat. Mus., Washington, D.C.

Description. — Large dactylogyrids which may possess occasional spicules or scale-like chitinizations. Length 0.999-1.256 mm., greatest body width 0.221-0.321 mm. Haptoral shape atypical and resembles that of *A. bursatus* (Mueller, 1936) and *A. bifurcatus* Mizelle, 1941, more than that of other members of the genus; haptoral width 0.221-0.357 mm., haptoral length 0.142 mm. Haptoral bars modified and articulated with each other as in other *Actinocleidus* species but peculiar in that each consists of two individual parts (Pl. 1, Figs. 55, 56). It is thought, however, that possibly this condition represents a variation and that the normal condition more nearly approaches that of other *Actinocleidus* species. The bars were clearly observable in only one of the two specimens. Anterior bar length 0.032 mm., posterior bar length 0.018 mm. Anchors similar in size and shape, bases bifurcate, and with regularly recurved hollow shafts and points; posterior pair usually a trifle larger (Pl. 1, Figs. 57-60). Length of anterior anchors 0.026-0.032 mm., width 0.009-0.011 mm.; posterior anchor length 0.032 mm., width of base 0.011-0.012 mm. Hooks fourteen in number, subequal in length, and normal in arrangement except that hooks of pairs six and seven lie unusually near the posterior edge of haptor and those of number six are more ventral than dorsal. Hooks of pair number five lie between the arms of the posterior bar. Each hook is differentiated into a relatively small ovoid base, a slender shaft, a sickle-shaped termination, and a strongly developed opposable piece (Pl. 1, Figs. 63, 64). A chitinous process which arises from the sickle-shaped termination and projects posteriorly is strongly developed in the present species. This structure can be observed in various degrees of development in practically all species of North American fresh-water Tetraonchinae and probably serves as an attachment for muscles which operate the hooks. Hook lengths 0.014-0.020 mm. Eye spots four, members of posterior pair larger and closer together than members of anterior pair. Cephalic lobes poorly developed; pharynx ovoid in outline but at times crescentic, transverse diameter 0.037-0.050 mm. Ovary pyriform in dorsal view and of moderate size, testis not clearly observed. Vagina not definitely observed but apparently unchitinized and situated sinistrally and marginally near the body midlength; seminal receptacle not apparent. Copulatory complex consisting of an irregularly sigmoid cirrus and a claw-like accessory piece (Pl. 1, Figs. 61, 62). Cirrus with a large base and a moderate-sized, obliquely truncate shaft. Accessory piece with a hollow basal portion and attached to the cirrus base. Cirrus length 0.044-0.046 mm., accessory piece length 0.035 mm. Vitellaria strongly developed and terminate posteriorly near the peduncle.

Relationships of this species are very interesting. It possesses a cirrus which somewhat resembles that of *A. maculatus* Mueller, 1937 (Fig. H-16 and Mizelle, 1941, Fig. 21). The accessory piece, however, is more nearly like that of *A. bifurcatus* Mizelle, 1941, (Figs. 44, 45). Neither of these species has been recovered from the gills of the large-mouth bass. The haptoral armament is interesting since (1) the anchors are similar to those of *A. bursatus* (Mueller 1936, Pl. 12, Fig. 7), (2) the bars are probably most closely related to *A. bifurcatus* (Mizelle 1941, Figs. 39, 40), and (3) the hooks, which are unlike those of either of these two above species, approach those of *A. flagellatus* (Mizelle and Seamster 1939, Fig. 41) in structure.

CLEIDODISCUS MIRABILIS Mueller, 1937

Pl. 2, Figs. 1-13

Hosts and Locality. — Black Bullhead, *Ameiurus melas* (Rafinesque), Channel Cat, *Ictalurus lacustris punctatus* (Rafinesque), Fulton Cat, *Ictalurus furcatus* (Le Sueur), Reelfoot Lake, Ridgely, Tennessee.

Previously Reported Host and Locality. — Mud Cat, *Pilodictis olivaris*, (Rafinesque), Mississippi River (Mueller 1937).

Specimens Studied.—Forty-nine.

Comparative Description. — Comparatively large dactylogyrids with a smooth cuticula. Length 0.986 mm. (0.621-1.290 mm.) "as much as 1.3 mm. long," body width 0.109 mm. (0.064-0.150 mm.) "about 0.185 mm. wide." Peduncle moderate to extremely long, haptor hexagonal in dorsal view. Haptor length 0.091 mm. (0.064-0.129 mm.), haptor width 0.092 mm. (0.057- 0.143 mm.). Haptoral bars dissimilar. Ventral bar usually bent posteriorly in middle, with rounded ends, and a short medial projection on the posterior border (Pl. 2, Figs. 12, 13). In many cases this structure is practically identical with that figured for *C. pricei* (Mueller, 1936a, Fig. 12). In other cases it resembles the bar figured for *C. floridanus* (*Ibid.*, Fig. 16) and that figured for itself (Mueller, 1937, Fig. J-50). Length of ventral bar 0.071 mm. (0.047-0.086 mm.). Dorsal bar varying between that figured for *C. pricei* and *C. floridanus* (Mueller, 1936a, Figs. 12 and 16). Dorsal bar length 0.074 mm. (0.044-0.108 mm.). "Bars about equal in size, . . . about 0.089 mm. long." Anchors similar in shape and size, usually with regularly recurved (solid) shafts and points. Bases infrequently bifurcate (Pl. 2, Figs. 1-5), variable in development, and ranging from that figured in the original description for *C. mirabilis* to those included herein. The ventral anchor shafts are generally noticeably bent in the direction of the points as is the case in *C. pricei* (Pl. 2, Figs. 2, 4, 5). This condition is less often observed in the dorsal anchors. Length of ventral anchors 0.056 mm. (0.038-0.069 mm.), width of bases 0.015 mm (0.007-0.026 mm.). Length of dorsal anchors 0.055 mm. (0.030-0.065 mm.), width of bases 0.014 mm. (0.009-0.021 mm.). "Anchors equal, about 0.073 mm. in greater dimension." Hooks subequal in length, normal in number and arrangement, and with morphology as shown for *C. floridanus* (Mueller,

1936a, Fig. 16). Hook bases usually tapered and those of pair five more ovoid in outline. Hook lengths 0.014-0.020 mm. Eye spots four, posterior pair larger and usually closer together than members of the anterior pair. Cephalic lobes well-developed, head organs conspicuous, pharynx circular to ovate in dorsal view. Transverse diameter of pharynx 0.041 mm. (0.029-0.050 mm.). Gonads situated near midportion of body; testis ovate in outline, longitudinally elongate, several times larger than, and situated posterior to, the ovately outlined ovary which has its posterior border overlapped by the anterior edge of the testis. Vagina sinistral and situated in anterior body half, seminal receptacle well developed. Copulatory complex consisting of a large distally inflated cirrus and ornate accessory piece. The cirrus is not unlike that of *C. floridanus* (Mueller, 1936a, Figs. 17, 18) and *C. mirabilis* (Mueller 1937, Figs. J-6, 7) and has a digitiform structure of variable length arising from its base. Cirrus length 0.073 mm. (0.051-0.100 mm.) "0.107 mm." Accessory piece variable and ranging in structure from that figured in original description to shapes shown in Pl. 2, Figs. 6-11. Accessory piece length 0.067 mm. (0.031-0.085 mm.) "0.089 mm." A relatively large prostate containing yellowish granular material was observed near the cirrus base; seminal vesicle well developed. Vitellaria well developed and terminate near the peduncle.

The present specimens are interesting since all the hosts from which they are recorded herein are new, and heretofore undescribed variations of a very striking nature are apparent. In most cases the ventral bar resembles that of *C. pricei* (and *C. floridanus*) which has been recorded from the above hosts. The anchors normally resemble those of *C. floridanus* in shape except that the shafts of the ventrals are usually bent in the direction of the points as recorded for *C. pricei*. The hooks are identical with those of *C. floridanus*. The copulatory complex is interesting since the principal difference between it and that of *C. floridanus* exists in the nature of the accessory piece which is strikingly variable morphologically. Normally it consists of a shaft and a distally located (1) knob, (2) leaflike structure, and (3) two hooked processes. In some cases the knob is vestigial or apparently wanting, in others the knob is double (Pl. 2, Fig. 11). Frequently, the leaf-like structure is absent (Pl. 2, Fig. 10), or present and turned, or developed so that the accessory piece apparently possesses three hooked terminations (Pl. 2, Figs. 6, 7, 9). Further studies may show *C. floridanus* and *C. mirabilis* to be identical.

CLEIDODISCUS PRICEI Mueller, 1936

Pl. 1, Figs. 65-74

Hosts and Locality. — Black Bullhead, *Ameiurus melas* (Rafinesque). Yellow Bullhead, *Ameiurus natalis* (Le Sueur), Channel Cat, *Ictalurus lacustris punctatus* (Rafinesque), Fulton Cat, *Ictalurus furcatus* (Le Sueur), Reelfoot Lake, Ridgely, Tennessee.

Previously Reported Hosts and Localities. — Channel Catfish, *Ictalurus lacustris punctatus* and Yellow Bullhead, *Ameiurus natalis*, Myakka River, Florida and Lake Okeechobee, Florida (Mueller 1936a). Brown Bullhead,

Ameiurus nebulosus, (Le Sueur), Myakka River, Florida and Lake Okeechobee, Florida (Mueller 1936a) and Oneida Lake, New York (Mueller 1937). Black Bullhead, *Ameiurus melas* (Rafinesque), Local Ponds and Streams near Stillwater, Oklahoma (Seamster 1938) and Baton Rouge, Louisiana (Summers and Bennett 1938).

Specimens Studied.—Thirty-eight.

Comparative Description.—Moderately large dactylogyrids with a smooth cuticula. Length 0.520 mm. (0.386-0.928 mm.) "0.620 mm.," body width 0.080 mm. (0.057-0.114 mm.) "0.140 mm." Peduncle moderate, haptor irregularly hexagonal to ovate in outline, haptor width 0.069 mm. (0.043-0.100 mm.), haptor length 0.076 mm. (0.050-0.107 mm.). Haptoral bars dissimilar (Mueller 1936a, Fig. 12) and variable (Pl. 1, Figs. 73, 74 and Seamster, 1938, Figs. 1-7). Ventral bar bent near midportion and with rounded ends, dorsal bar with an ornate anterior surface (of variable length and height) which is at times apparently smooth. Ventral bar length 0.042 mm. (0.028-0.047 mm.) "0.050 mm.," dorsal bar length 0.045 mm. (0.029-0.052 mm.) "0.058 mm." Anchors typically similar in size and shape and with regularly recurved solid shafts and points. Anchor bases bifurcate, superficial roots longer than deep roots (Pl. 1, Figs. 65, 66). This observation differs from that portrayed by the figure accompanying the original description (Mueller, 1936a, Fig. 12) in which the bases are nonbifurcate and the deep roots are vestigial. Frequently one or both pairs of the anchors have the superficial roots reduced to the extent that they approach the shape of the anchors of *C. floridanus* (Pl. 1, Figs. 67, 69) and (Mueller, 1936a, Fig. 16). Seamster in 1938 noticed similar variations (Fig. 7) in this species. In addition to this variation, wide discrepancy in the size of the two pairs of anchors was observed by Seamster and also in the present work (Pl. 1, Figs. 71, 72). This type of variation has apparently given rise to the "*Haplocleidus*" species within the genus *Urocleidus* Mueller, 1934. Ventral anchor length 0.044 mm. (0.034-0.054 mm.), width 0.011 mm. (0.008-0.016 mm.). Dorsal anchor length 0.048 mm. (0.035-0.074 mm.), width 0.012 mm. (0.008-0.017 mm.). "Greatest straight line measurement of a large hook, 0.048 mm." Hooks fourteen in number, subequal in length, and normal in arrangement. They exist as shown by Mueller (1936a, Fig. 12) except that (1) an opposable piece is present, (2) hook points of pair number one are directed anteriorly, and (3) those of pair number five point posteriorly and lie between the ventral anchor shafts. Hook lengths 0.013-0.018 mm. "about 0.016 mm." Eye spots four, members of posterior pair larger than those of anterior pair, spatial relationships between members of each pair variable. Cephalic lobes small; pharynx circular to ovate in outline, transverse diameter 0.030 mm. (0.024-0.041 mm.) "0.040 mm." Gonads situated near middle of body; ovary elliptical in outline and at times very elongate, testis moderately ovate and situated immediately posterior to ovary. Vagina, seminal vesicle, and seminal receptacle not observed. Copulatory complex as described originally (Mueller, 1936, Figs. 13-15). Cirrus length 0.034 mm. (0.025-0.054 mm.) "0.037 mm.," accessory piece length 0.032 mm. (0.022-0.055 mm.).

UROCLEIDUS ATTENUATUS Mizelle, 1941

Host and Locality.—Red-Eared or Stumpknocker Sunfish *Lepomis microlophus* (Günther), Reelfoot Lake, Ridgely, Tennessee.

Previously Reported Hosts and Localities.—Stumpknocker Sunfish, *Lepomis microlophus* (Günther), Englewood Pond, Englewood, Florida; Everglades Canal, Naples, Florida; and Lake Okeechobee, Moore Haven, Florida (Mizelle 1941). Bluegill Sunfish, *Lepomis macrochirus* (Rafinesque) Canal, North Everglades, Florida (Mizelle and Brennan 1942). Western Spotted Sunfish, *Lepomis miniatus* Jordan, Reelfoot Lake, Ridgely, Tennessee (Mizelle and Jaskoski 1942).

Specimens Studied.—Three.

Nine specimens were used in the determination of structures and their sizes in the original description in contrast to three specimens which were available in this work. Since some of the minima and maxima obtained herein are outside those published in the original description, it is thought worthwhile mentioning them. Measurements for minima which were below those referred to above, are as follows: (1) body width 0.100 mm. "0.108 mm.," (2) haptor width 0.086 mm. "0.095 mm.," (3) dorsal bar length 0.024 mm. "0.026 mm.," (4) ventral anchor width 0.014 mm. "0.016 mm.," and (5) cirrus length 0.076 mm. "0.081 mm." The maximum measurements which were greater than those originally reported are: (1) haptor length 0.0100 mm. "0.083 mm.," (2) ventral anchor width 0.026 mm. "0.024 mm.," (3) dorsal anchor length 0.031 mm. "0.030 mm.," (4) cirrus length 0.101 mm. "0.096 mm.," and (5) transverse diameter of pharynx 0.054 mm. "0.053 mm." The Florida specimens averaged less in length (0.765 mm.) than those from Tennessee (0.828 mm.). The hooks of pair number five are situated between the ventral pair of anchors and the haptor which was originally described as subquadrate in outline and was observed in the present work to be of pentagonal outline with the posterior side rounded.

The dorsal bar was found to possess a raised central portion on the anterior surface remotely resembling that figured for the ventral bar (Mizelle 1941, Fig. 34) and to possess very irregular serrate margins.

The copulatory complex was observed to agree with the original description except for the fact that it seems to be undulate or, at best, coiled to only a slight degree and there is a cirral thread present on the cirrus shaft and in some cases this structure (cirral thread) is relatively very large proximally. A cirral thread was reported for this species taken from *Lepomis miniatus* by Mizelle and Jaskoski (1942). A relatively large, broadly fusiform (longitudinally elongate) seminal vesicle and a well-developed but smaller seminal receptacle were observed. The latter structure is situated posterior to the former. A conspicuous prostate filled with yellowish granular material was also observed. The accessory piece was observed to be of characteristic shape but apparently more highly chitinized than in previously observed specimens.

UROCLEIDUS CHAENOBRYTTUS Mizelle and Seamster, 1939

Pl. 2, Figs. 54-63

Host and Locality. — Warmouth Bass, *Chaenobryttus coronarius* (Bartram), Reelfoot Lake, Ridgely, Tennessee.

Previously Reported Hosts and Localities. — Warmouth Bass, *Chaenobryttus coronarius* (Bartram), Roadside Canal, Naples, Florida; Roadside Ditch, Englewood, Florida; and Woodmere Pond, Englewood, Florida (Mizelle and Seamster 1939). Western Spotted Sunfish, *Lepomis miniatus* Jordan, Reelfoot Lake, Tennessee (Mizelle and Jaskoski 1942).

Specimens Studied.—Twenty.

The Tennessee specimens in regard to structure agree with those from Florida which were used in the original description except that (1) the posterior eye spots are not always closer together than members of the anterior pair, and (2) a well-defined accessory piece is present in the copulatory complex (Pl. 2, Fig. 54). In addition there are certain size differences which are interesting (Table 4). The average measurements for specimens from the two localities were larger in the more northern forms (Tennessee) except for (1) haptoral width (2) dorsal bar length and (3) dorsal and ventral anchor widths. In the case of the body length, the minimum for the Tennessee forms was larger than the maximum for the Florida representatives and in addition the minimum and maximum for width were greater than corresponding measurements for Florida forms. This agrees with the statement by Mizelle (1940) that the northern forms of North American fresh-water Tetraonchinae are generally larger than the southern specimens of the same species. This statement, however, is not always true for the internal structure of these parasites. In making conclusions of this kind, the question naturally arises as to what constitutes a representative sample. Obviously the picture might be altered were the data forthcoming from as many specimens (20) as were available in the Tennessee material.

UROCLEIDUS DISPAR (Mueller, 1936)

Synonym. — *Onchocleidus dispar* Mueller, 1936; *Haplocleidus dispar* (Mueller, 1936) Mueller, 1937.

Host and Locality. — Large-Mouth Bass, *Huro salmoides* (Lacépède), Reelfoot Lake, Ridgely, Tennessee.

Previously Reported Hosts and Localities.—Pumpkinseed Sunfish, *Lepomis gibbosus* (Linnaeus), Constantia, New York (Mueller 1936). Bluegill Sunfish, *Lepomis macrochirus*, Rafinesque, Local Streams and Ponds near Stillwater, Oklahoma (Seamster 1938); and Various Localities in Illinois (Mizelle 1938a). Orange-Spotted Sunfish, *Lepomis humilis* (Girard), Local Ponds and Streams near Stillwater, Oklahoma (Seamster 1938).

Specimens Studied.—One.

It is thought that the single specimen recovered here from the large-mouth bass is ectopic for this host since it is extremely infrequent that a species of Tetraonchinae is found on the large-mouth bass and also on any of the reported hosts listed above. Length 0.650 mm. "0.500 mm.," greatest body width 0.086 mm. The shape of the haptor is difficult to describe since *"Haplocleidus"* forms have the anchors differentiated so that they cause it (haptor) to lie on its side. It is presumed that in dorsal view it is pentagonal or hexagonal in outline which is generally the case in most species of *Urocleidus*. Haptor width 0.057 mm., length 0.071 mm. The bars are dissimilar and the ventral bar resembles that figured in the original description except that it appears to be spined. The dorsal bar is mildly of dumb-bell shape and somewhat similar to that of *U. parvicirrus* described in the present work, in that the ends are interrupted by a groove. Ventral bar length 0.014 mm., dorsal bar length 0.023 mm. Anchors exist as shown by Mueller (1936, Pl. 13, Fig. 11); ventral anchor length 0.036 mm. "0.040 mm.," width of bases 0.014 mm. Dorsal anchor length 0.069 mm. "0.080 mm.," width of bases 0.011 mm. Hooks normal in number and arrangement and each, except members of pair number five, possesses 1) an elliptical base as long as, or longer than, 2) the slender shaft, 3) a sickle-shaped termination, and 4) an opposable piece. Hooks of pair number five have the same morphology as the rest of the hooks except that they have bases which are shorter than the shafts. Hooks of pair number five are somewat shorter than the rest which are subequal in length, hook lenghts 0.014-0.017 mm. Eye spots four and fragile; members of the posterior pair larger than those of the anterior pair. Cephalic lobes small; pharynx ovoid in outline, transverse diameter 0.043 mm. "0.020 mm."

Copulatory complex as originally described (Mueller 1936, Pl. 14, Fig. 24). The "sculptured" nature of the cirrus shaft is apparently due to the presence of a pair of cirral threads which are wound tightly around it. Cirrus 0.026 mm. "0.025 mm." Vitellaria sparsely developed and do not extend to the peduncle.

UROCLEIDUS GRANDIS Mizelle and Seamster, 1939

Pl. 2, Figs. 47-53

Host and Locality. — Warmouth Bass, *Chaenobryttus coronarius* (Bartram), Reelfoot Lake, Ridgely, Tennessee.

Previously Reported Host and Localities. — Warmouth Bass, *Chaenobryttus coronarius* (Bartram), Roadside Canal, Naples, Florida and Woodmere Pond, Englewood, Florida (Mizelle and Seamster 1939).

Specimens Studied.—Twenty.

Specimens of *U. grandis* from Tennessee agree with those from Florida which were used in the original description except that (1) the projection on the anchor shafts seem to be somewhat modified (Pl. 2, Figs. 47, 48 and Mizelle and Seamster 1939, Figs. 3, 4), (2) the dorsal anchor bases are not folded to one side and are apparently somewhat shorter, and (3) the cirrus

at times appears to be narrower at the base and to possess a well-defined accessory piece (Pl. 2, Figs. 52, 53) which was not figured in the original description (Mizelle and Seamster 1939, Fig. 5). As in *A. flagellatus* and *U. chaenobryttus* the sample from Florida is admittedly small, the average body length is smaller than that for the Tennessee forms, and the body width is also greater in the latter specimens. See Table 5 for comparison of other measurements.

UROCLEIDUS PARVICIRRUS Mizelle and Jaskoski, 1942

Host and Locality.—Red-Eared or Stumpknocker Sunfish, *Lepomis microlophus* (Günther), Reelfoot Lake, Ridgely, Tennessee.

Previously Reported Host and Locality. — Western Spotted Sunfish, *Lepomis miniatus* Jordan, Reelfoot Lake, Ridgely, Tennessee (Mizelle and Jaskoski 1942).

Specimens Studied.—Five.

This is the first time that specimens of this species have been recovered since the publication of the original description by Mizelle and Jaskoski (1942). Morphologically they agree with those used for the original description except that (1) the dorsal bar tends to have more rounded ends which are cleft and (2) for certain size differences. The latter is to be expected since the original description was made from two specimens. Length 0.564 mm. (0.545-0.638 mm.) "0.423-0.465 mm.," greatest body width 0.073 mm. (0.063-0.078 mm.) "0.085 mm." Haptor length 0.076 mm. (0.072-0.086 mm.) "0.067 mm.," haptor width 0.059 mm. (0.049-0.063 mm.). Dorsal bar length 0.027-0.029 mm., "0.021-0.026 mm." Ventral bar length 0.016-0.21 mm. "0.018 mm." Ventral anchor length 0.040 mm. (0.034-0.043 mm.) "0.036-0.040 mm.," ventral anchor width 0.010 mm. (0.009-0.011 mm.) "0.011 mm." Dorsal anchor length 0.074 mm. (0.063-0.080 mm.) "0.071-0.073 mm.," dorsal anchor width 0.014 mm. (0.012-0.017 mm.) "0.013 mm." Cirrus length 0.027 mm. (0.022-0.036 mm.) "0.028 mm." Accessory piece length 0.018 mm. (0.016-0.020 mm.) "0.014 mm." Hook lengths 0.013-0.020 mm. "0.014-0.020 mm." Pharynx diameter (transverse) 0.029 mm. (0.025-0.031 mm.) "0.030-0.033 mm."

This species possesses an accessory piece similar to that of *U. furcatus* (Mueller 1937, Fig. E-12) and *U. dispar* (Mueller 1936, Pl. 14, Fig. 24) but differs from the above species by the presence of a short unsculptured cirrus resembling that of *U. perdix* (Mueller 1937, Fig. B-9). The presence of a vagina and the morphology of the haptoral hooks provide further differences between *U. parvicirrus* and *U. dispar* (see Mueller 1936, Pl. 13, Fig. 11 and Mizelle and Jaskoski 1942, Figs. 67-69).

UROCLEIDUS PRINCIPALIS (Mizelle, 1936)

Synonyms.—Onchocleidus principalis, Mizelle, 1936 *Onchocleidus contortus* Mueller, 1937.

Host and Locality. — Large-Mouth Bass, *Huro salmoides* (Lacépède), Reelfoot Lake, Ridgely, Tennessee.

Previously Reported Hosts and Localities. — Kentucky or Spotted Bass, *Micropterus punctulatus* (Rafinesque), Salt Fork of the Big Vermilion River, Homer, Illinois (Mizelle, 1936); Cove Creek, Caryville, Tennessee; Norris Lake, Norris, Tennessee, and Cold Creek, Below Norris Dam (Tennessee) (Mizelle 1940). Small-Mouth Bass, *Micropterus dolomieu* Lacépède, Local Ponds and Streams near Stillwater, Oklahoma (Seamster 1938); Salt Fork of the Big Vermilion River, Homer, Illinois (Mizelle 1938a); and Cove Creek, Caryville, Tennessee (Mizelle 1940). Large-Mouth Bass, *Huro salmoides* (Lacépède), Florida (Mueller 1937); Baton Rouge, Louisiana (Summers and Bennett 1938); Lake Senachwine, Henry, Illinois (Mizelle 1938a); and Hatchery, Norris, Tennessee (Mizelle 1940).

Specimens Studied. Nine.

This species is easily recognizable by its moderately small size, characteristic haptoral armament (anchors, bars, hooks), and the corkscrew-like cirrus which is provided with an accessory piece which is generally bifurcate distally to form two prongs which pass one on each side of the cirrus. Occasionally the prongs unite to produce a hole through which the cirrus passes (Mizelle 1938a, Pl. 4, Fig. 81, and Mueller 1937, Fig. A-15). The measurements obtained from the nine specimens studied in this work agree with those given in a comparative description by Mizelle (1940) except that the minima for body width, 0.057 mm. "0.070 mm.," and dorsal bar length 0.029 mm. "0.030 mm.," are less and maxima for (1) dorsal anchor length 0.046 mm. "0.041 mm.," (2) cirrus length, 0.052 mm. "0.049 mm.," and (3) accessory piece length, 0.031 mm. "0.028 mm." are greater. The specimens for the same host in Florida averaged much shorter (0.237 mm.) than those in this work (0.396 mm.)

Urocleidus torquatus n. sp.

Pl. 2, Figs. 14-29

Host and Locality.—Red-Eared or Stumpknocker Sunfish, *Lepomis microlophus* (Günther), Reelfoot Lake, Ridgely, Tennessee.

Specimens Studied.—Seventeen.

Type Specimens.—Cotypes, U.S. Nat. Mus., Washington, D.C.

Description. — Moderately small dactylogyrids with a smooth cuticula. Length 0.432 mm. (0.343-0.528 mm.), greatest body width 0.055 mm. (0.043-0.064 mm.). Peduncle generally short and broad. Haptor pentagonal to hexagonal in dorsal view. Haptor width 0.063 mm. (0.050-0.093 mm.), length 0.076 mm. (0.064-0.093 mm.). Haptoral bars dissimilar and each with a spine on the posterior surface which is visible only in side view (Pl. 2, Figs. 18, 19). Ventral bar with rounded to obliquely truncate ends and bent posteriorly in the midportion (Pl. 2, Figs. 20, 21), length 0.025 mm. (0.022-0.031 mm.). Dorsal bar more robust, posterior surface bulged, ends rounded to

obliquely truncate, and with a perforation near the midportion which often opens to produce a notch (Pl. 2, Fig. 22), length 0.026 mm. (0.020-0.028 mm.). Anchors with solid points and shafts which unite to form an angle, similar in shape and size, and each with a protuberance on the terminal part of the shaft (Pl. 2, Figs. 14-17). Anchor bases slightly bifurcate, superficial roots much longer than deep roots. Length of ventral anchors 0.049 mm. (0.043-0.056 mm.), width of bases 0.009 mm. (0.007-0.011 mm.). Length of dorsal anchors 0.048 mm. (0.041-0.054 mm.), width of bases 0.010 mm. (0.007-0.011 mm.). Hooks fourteen in number and normal in arrangement. Hooks of pair number five comparatively small (0.009-0.013 mm.) and situated between the ventral anchor shafts. These hooks usually do not possess a base (Pl. 2, Fig. 27) but infrequently a suggestion of one is evident (Pl. 2, Fig. 29). Each of the other hooks is composed of a slender or stout shaft, a sickle-shaped termination and a well-defined opposable piece (Pl. 2, Fig. 28). Hooks (except those of pair number five) subequal in length and with members of pairs numbers one, two, and seven somewhat larger than the rest; length 0.027-0.036 mm. Eye spots four, members of the posterior pair larger and much closer together (often contiguous) than those of the anterior pair. Cephalic lobes vestigial or wanting, pharynx ovate (longitudinally elongate) in dorsal outline and often rotated from the normal alignment, transverse diameter 0.019 mm. (0.017-0.021 mm.). Gonads not observed, vagina apparently wanting, seminal vesicle bulb shaped and relatively large. Copulatory complex consisting of an attenuate cirrus and a sleeve-like accessory piece which is open on one side. Cirrus comparatively straight with two cirral threads around its shaft (Pl. 2, Figs. 23, 24). Cirrus length 0.031 mm. (0.026-0.035 mm.). Accessory piece in reality a chitinized portion of the vestibule (cirrus sac), (Pl. 2, Figs. 25, 26). Accessory piece length 0.020 mm. (0.017-0.022 mm.). Vitellaria moderately to greatly developed and infrequently a few follicles extend into the basal portion of the peduncle.

The closest relative of this species is *Urocleidus variabilis* n. sp. *U. torquatus* differs from its closest relative in the possession of (1) a greater average cirrus length (0.031 mm. as opposed to 0.027 mm.), (2) smaller haptoral hooks (0.027-0.036 mm. as opposed to 0.032-0.042 mm.), (3) anchors with more slender bases (Pl. 2, Figs. 14-17, 30-33), and (4) the presence of an enlarged terminal portion on each anchor shaft (Pl. 2, Figs. 14-17). This latter character is found in *Cleidodiscus longus* Mizelle, 1936, and *Urocleidus distinctus* (Mizelle, 1936). It serves to distinguish immediately *U. torquatus* from its nearest relative, *U. variabilis*.

Urocleidus variabilis n. sp.

Pl. 2, Figs. 30-46

Host and Locality.—Red-Eared or Stumpknocker Sunfish, *Lepomis microlophus* (Günther), Reelfoot Lake, Ridgely, Tennessee.

Specimens Studied.—Twenty.

Type Specimens.—Cotypes, U.S. Nat. Mus., Washington, D.C.

Description. — Moderately small dactylogyrids with a smooth cuticula. Length 0.456 mm. (0.336-0.578 mm.), greatest body width 0.059 mm. (0.043-0.093 mm.). Peduncle short and broad to moderately slender. Haptor pentagonal in dorsal view, posterior end rounded, width 0.109 mm. (0.043-0.113 mm.), length 0.076 mm. (0.050-0.107 mm). Haptoral bars dissimilar and each possesses a spine on the posterior border which is visible only in side view (Pl. 2, Figs. 34, 35). Ventral bar with rounded ends, slightly bent posteriorly in the midportion, and somewhat variable in shape (Pl. 2, Figs. 36, 38), length 0.029 mm. (0.026-0.033 mm.). Dorsal bar more robust, broadly bent in the middle, ends rounded (often moderately ornate) and with a perforation near the midportion (Pl. 2, Figs. 37, 39). Dorsal bar length 0.025 mm. (0.023-0.031 mm.). Anchors generally with regularly recurved (solid) shafts and points, similar in size and shape, and with slightly bifurcate bases (Pl. 2, Figs. 30-33). Length of ventral anchors 0.042 mm. (0.036-0.049 mm.), width of bases 0.010 mm. (0.007-0.013 mm.). Length of dorsal anchors 0.042 mm. (0.035-0.051 mm.), width of bases 0.011 mm. (0.009-0.013 mm.). Hooks fourteen in number, and normal in arrangement (Mizelle 1938a). Hooks of pair number five comparatively small, 0.009-0.013 mm. in length, with or without well-defined subspherical bases (Pl. 2, Figs. 44, 46), and situated between the ventral anchor shafts. Each hook (except those of pair number five) composed of a slender-to-stout shaft, a sickle-shaped termination and a conspicuous opposable piece (Pl. 2, Fig. 45). Hooks (except member of pair number five) subequal in length with members of pairs one, six, and seven somewhat larger than the rest; lengths 0.032-0.042 mm. Eye spots four, members of posterior pair larger and situated closer together than those of the anterior pair. Posterior eye spots infrequently united with each other. Cephalic lobes poorly developed or lacking. Pharynx broadly ovate in dorsal outline and with long axis parallel to body axis; pharynx diameter 0.021 mm. (0.017-0.024 mm.). Gonads not observed, vagina apparently lacking, seminal vesicle well developed. Copulatory complex consisting of an attenuate cirrus and a sleeve-like accessory piece which is open on one side (Pl. 2, Figs. 40-43). Cirrus straight with a comparatively small base and a cirral thread around the shaft, cirrus length 0.027 mm. (0.023-0.031 mm.). Accessory piece in reality a chitinized portion of the vestibule (cirrus sac); accessory piece length 0.020 mm. (0.016-0.026 mm.). Vitellaria moderately to greatly developed, consisting of follicles of different sizes which generally extend into the basal portion of the peduncle and infrequently into the proximal part of the haptor.

The closest relative of this species is *Urocleidus torquatus* n. sp. Differences between the two species are enumerated under the description of *U. torquatus*. Obviously, these two species are very similar but the differences noted seem adequate for specific separation.

Discussion

The problem concerning the effect of the host on the size and number of parasites harbored is interesting and also very complicated. Chandler (1939)

observed that the size of *Hymenolepis diminuta* in the rat (*Mus norvegicus*) varied inversely as the number of specimens harbored. This phenomenon was attributed to "crowding effects" concerned with nutritional phenomena (Chandler 1943) and not to an immunity as commonly understood. The danger of comparing phenomena regarding endoparasites (intestinal tapeworms) with those presented by ectoparasites (gill trematodes) is recognized. Nevertheless, observations regarding *Cleidodiscus pricei* and *C. mirabilis* are thought interesting enough for comparison with Chandler's observations. In the case of the former species, specimens were available from four fishes, namely, the yellow bullhead, Fulton cat, black bullhead, and the channel cat. The material from these hosts was infected with different numbers of *C. pricei* and the average length of the parasites varied inversely as the number of specimens harbored (Table 3) which agrees with Chandler's observations. However, in the present work there is no knowledge of (1) the numbers of hosts specimens involved, (2) possible differential host susceptibility which might be operative, and (3) the age of the hosts which Ackert (1942) thinks important in the case of many parasites. The question also arises as to the probable effects of other parasites present, for which no information is available in the present work. Mizelle (1938a) observed significant differences in the size of *Urocleidus mucronatus* from bluegill hosts in two lakes in Illinois and was later (1940) stimulated to record latitudinal variations for several species of Tetraonchinae but did not consider the complicating factors as the crowding effects of Chandler, the age of the hosts (Ackert 1942), or possible immunity as determined by Kimpel (1940).

The case of *C. mirabilis* is possibly less pronounced than that of *C. pricei* (Table 2). Only three host species (number of specimens unknown) were involved in this case and the results do not agree with those for *C. pricei*. In fact the average body length of the twenty parasites from the black bullhead was greater than that for the ten specimens from the Fulton catfish and 0.068 mm. less than that for the nineteen specimens from the channel cat. It is very obvious that here the question of host specificity may be an important factor. The criteria to be used in judging the suitability of hosts for a given species of parasite become perplexing. Other things being equal, it seems that the number of specimens harbored or the size of the infesting specimens or both could be used.

As mentioned before, Mizelle (1938a) noted wide size differences in specimens of *Urocleidus mucronatus* which he thought were possibly due to phenomena concerned with latitude. In 1940 he observed that in most of the cases involving comparison of specimens of several species of Tetraonchinae from north and south localities, the body size of the northern representatives was larger than that of specimens from southern localities. Notwithstanding the complicating factors noted above, the data derived in the present work support these conclusions except in the case of (1) *U. dispar* which is considered ectopic for the large-mouth bass, (2) *C. pricei* which averaged less in length but had a larger maximum length, and possibly (3) *C. mirabilis* which was taken from the Mississippi River at a place not specified by the original

author. It is not known how many specimens were used by Mueller in the original description of *U. dispar*, *C. pricei* and *C. mirabilis*.

The red-eared or stumpknocker sunfish from Florida, which harbors five species of Tetraonchinae, (Mizelle 1941) is infested with eight species in Reelfoot Lake and only one (*Urocleidus attenuatus*) of these has been previously recorded for the same host species in Florida. *Urocleidus parvicirrus* Mizelle and Jaskoski, 1942, which was described from the western spotted sunfish (*Lepomis miniatus*) was found to occur on this host in the present work. The remaining six of the eight species are new. *U. dispar* (Mueller, 1936) is a new record for the large-mouth bass and is thought by the present authors to be ectopic for this host. The black bullhead, channel cat, Fulton cat, and the yellow bullhead are new hosts for *Cleidodiscus mirabilis* Mueller, 1936(a).

Reelfoot Lake constitutes a new geographical record for all previously described species in this work except *Urocleidus attenuatus* and *U. parvicirrus*. These two species of Tetraonchinae also occur on the western spotted sunfish (*L. miniatus*) in this habitat.

Summary

Twenty-seven vials of piscine branchial material which had been frozen and preserved in five per cent formalin were examined. The gill material was taken from eight host species, namely, *Ameiurus melas* (Rafinesque), *A. natalis* (Le Sueur), *Amia calva* Linnaeus, *Ictalurus furcatus* (Le Sueur), *I. lacustris punctatus* (Rafinesque), *Huro salmoides* (Lacépède), *Lepomis microlophus* (Günther), and *L. miniatus* Jordan. All of the host material except that from *Amia calva* was infected. The descriptions of the parasites from *L. miniatus* were published by Mizelle and Jaskoski in 1942.

Measurements and figures of parasites were made microscopically with a calibrated ocular micrometer and a camera lucida respectively. A total of four hundred specimens, representing seven new and ten previously described species, were recovered from the host material. Of these, two hundred thirteen were observed and measured. The new species (*Actinocleudis bakeri, Actinocleidus bifidus, Actinocleidus crescentis, Actinocleidus harquebus, Actinocleidus unguis, Urocleidus torquatus,* and *Urocleidus variabilis*) were described and the previously described species (*Actinocleidus flagellatus, Actinocleidus fusiformis, Cleidodiscus mirabilis, Cleidodiscus pricei, Urocleidus attenuatus, Urocleidus chaenobryttus, Urocleidus dispar, Urocleidus grandis, Urocleidus parvicirrus,* and *Urocleidus principalis*) were comparatively described. Type specimens of the new species will be deposited in the Helminthological Collection of the United States National Museum, Washington, D. C.

In *C. pricei* the size of the parasites varied inversely as the number of specimens harbored by different host species. Size variations for all previously described species generally present a larger body size for the more northern

representatives of a given species. *Lepomis microlophus* from Reelfoot Lake harbors eight species, six of which are new. The same host species from Florida was found infested with five species of parasites (Mizelle 1941) only one (*U. attenuatus*) of which was recovered from the Reelfoot Lake host. The other species (*U. parvicirrus*) was described from the western spotted sunfish (*Lepomis miniatus*) by Mizelle and Jaskoski (1942).

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EXPLANATION OF TABLES: AP, Accessory piece; A, Anterior; AL, Anterior bar length; C, Cirrus; D, Dorsal; DL, Dorsal bar length; L, Length; Ph, Pharynx (transverse diameter); P, Posterior; PL, Posterior bar length; V, Ventral; VL, Ventral bar length; W, Width. Measurements are given in microns.

TABLE 1.—Measurements of *Actinocleidus flagellatus* from different localities. (Host, Warmouth Bass)

1. Tennessee Locality—Reelfoot Lake, Ridgely, Tennessee—Eight specimens.
2. Florida Localities—Roadside Canal and Roadside Ditch, Englewood, Florida—Three specimens.

		Haptor				Bars		Anchors A		Anchors P			
		L	W	L	W	AL	PL	L	W	L	W	C	AP
1.	Min.	321	57	50	50	38	23	26	8	25	8	48	43
	Max.	472	100	72	86	53	29	35	12	35	17	56	58
	Ave.	388	74	56	66	44	26	32	9	30	11	51	49
2.	Min.	230	50	30	48	31	26	27	10	21	8	50	
	Max.	284	90	46	62	38	29	30	11	28	11	59	
	Ave.	269	69	38	57	35	28	28	10	25	9	55	

TABLE 2.—Measurements of *Cleidodiscus mirabilis* from Reelfoot Lake fishes

1. Black Bullhead Host—Twenty specimens.
2. Channel Cat Host—Nineteen specimens.
3. Fulton Cat Host—Ten specimens.
4. Composite average of the measurements of the forty-nine specimens recorded in this Table.

					Haptor		Bars		Anchors V		Anchors D			
		L	W	Ph	L	W	VL	DL	L	W	L	W	C	AP
1.	Min.	685	100	29	71	71	54	61	54	12	52	11	51	40
	Max.	1,085	150	44	121	136	86	108	69	26	65	21	100	85
	Ave.	862	123	38	100	111	76	84	62	18	59	16	79	70
2.	Min.	621	64	44	71	57	47	54	39	7	48	9	45	53
	Max.	1,290	128	50	129	143	79	76	61	19	59	19	82	76
	Ave.	930	93	47	89	91	70	68	53	13	54	13	67	65
3.	Min.	635	93	29	64	64	51	44	38	8	30	9	36	31
	Max.	1,114	129	36	100	136	80	66	54	15	60	14	74	81
	Ave.	860	110	33	82	96	64	59	46	12	50	11	63	65
4.	Min.	621	64	29	64	57	47	44	38	7	30	9	51	31
	Max.	1,290	150	50	129	143	86	108	69	26	65	21	100	85
	Ave.	986	109	41	91	92	71	74	56	15	55	14	73	67

TABLE 3.—Measurements of *Cleidodiscus pricei* from Reelfoot Lake fishes.

1. Yellow Bullhead Host—Sixteen specimens.
2. Fulton Cat Host—Ten specimens.
3. Black Bullhead Host Nine specimens.
4. Channel Cat Host—Three specimens.
5. Composite Average of the measurements of the thirty-eight specimens recorded in this Table.

					Haptor		Bars		Anchors V		Anchors D			
		L	W	Ph	L	W	VL	DL	L	W	L	W	C	AP
1.	Min.	386	57	24	57	43	28	29	34	8	35	8	25	22
	Max.	671	114	32	100	79	51	47	54	16	74	17	54	55
	Ave.	436	76	27	74	61	41	40	37	11	43	10	34	31
2.	Min.	407	64	24	50	43	34	32	37	8	40	9	29	27
	Max.	621	93	29	107	93	53	46	51	14	52	15	44	42
	Ave.	508	79	26	73	70	46	41	44	10	48	13	35	32
3.	Min.	478	57	31	71	64	39	39	45	11	47	13	29	31
	Max.	721	114	41	100	100	58	52	54	16	59	16	39	44
	Ave.	610	91	34	79	79	51	45	50	13	55	14	35	35
4.	Min.	635	64	26	71	64	37	35	48	13	44	13	30	25
	Max.	928	79	29	93	71	47	46	50	14	54	15	31	35
	Ave.	738	71	....	84	69	....	....	....	....	....	....	....	....
5.	Min.	386	57	24	50	43	28	29	34	8	35	8	25	22
	Max.	928	114	41	107	100	47	52	54	16	74	17	54	55
	Ave.	520	80	30	76	69	42	45	44	11	48	12	34	32

TABLE 4.—Measurements of *Urocleidus chaenobryttus* from different localities (Host, Warmouth Bass)

1. Tennessee Locality—Reelfoot Lake, Ridgely, Tennessee— Twenty specimens.
2. Florida Localities—Roadside Canal, Naples, Florida; Roadside Ditch, Englewood, Florida; and Woodmere Pond, Englewood Florida—Six specimens.

				Haptor		Bars		Anchors V		Anchors D		
		L	W	L	W	VL	DL	L	W	L	W	C
1.	Min.	463	64	72	57	25	23	61	8	63	10	74
	Max.	750	121	107	93	31	32	78	13	78	13	107
	Ave.	598	90	90	74	27	26	69	12	69	12	95
2.	Min.	245	52	67	54	24	26	57	12	57	13	55
	Max.	380	108	94	86	26	29	68	15	64	18	67
	Ave.	325	87	81	77	25	28	63	14	62	15	60

TABLE 5.—Measurements of *Urocleidus grandis* from different localities. (Host, Warmouth Bass)

1. Tennessee Locality—Reelfoot Lake, Ridgely, Tennessee— Twenty specimens.
2. Florida Localities—Roadside Canal, Naples, Florida, and Woodmere Pond, Englewood, Florida,—three specimens.

		Haptor		Bars			Anchors V		Anchors D		
		L	W	L	W	VL	DL	L	W	L	W	C
1.	Min.	386	64	50	57	21	28	41	12	50	11	64
	Max.	571	128	78	93	35	38	66	16	69	16	84
	Ave.	487	92	65	76	29	33	49	14	60	13	72
2.	Min.	257	60	60	64	30	30	43	17	57		41
	Max.	595	97	75	96	39	37	51	21	66		47
	Ave.	395	82	65	81	36	34	47	19	62		44

PLATE 1

All figures were drawn at the same magnification with the aid of a camera lucida.

Figs. 1-10. *Actinocleidus bakeri* n. sp. 1, Anterior bar. 2, Posterior bar. 3, Vagina. 4, Hooks. 5, Accessory piece. 6, Cirrus. 7, 9, Anterior anchors. 8, 10, Posterior anchors.

Figs. 11-27. *Actinocleidus bifidus* n. sp. 11, 12, Anterior bars. 13, 14, 15, Posterior bars. 16, 17, 18, Cirri. 19, 20, 21, Accessory pieces. 22, 23, Vaginae. 24, Anterior anchor. 25, Posterior anchor. 26, 27, Hooks.

Figs. 28-37. *Actinocleidus flagellatus* Mizelle and Seamster, 1939. 28, Anterior bar. 29, Posterior bar. 30, Anterior anchor. 31, Posterior anchor. 32, 33, Accessory pieces. 34, 35, Cirri. 36, 37, Hooks.

Figs. 38-46. *Actinocleidus harquebus* n. sp. 38, Anterior bar. 39, Posterior bar. 40, Cirrus. 41, Accessory piece. 42, Vagina. 43, Anterior anchor. 44, Posterior anchor. 45, 46, Hooks.

Figs. 47-54. *Actinocleidus crescentis* n. sp. 47, Anterior bar. 48, Posterior bar. 49, Cirrus. 50, Accessory piece. 51, Anterior anchor. 52, Posterior anchor. 53, 54, Hooks.

Figs. 55-64. *Actinocleidus unguis* n. sp. 55, Anterior bar. 56, Posterior bar. 57, 58, Anterior anchors. 59, 60, Posterior anchors. 61, Cirrus. 62, Accessory piece. 63, 64, Hooks.

Figs. 65-74. *Cleidodiscus pricei* Mueller, 1936. 65, 67, 70, 72, Ventral anchors. 66, 68, 69, 71, Dorsal anchors. 73, Ventral bar. 74, Dorsal Bar.

PLATE 2

All figures were drawn at the same magnification with the aid of a camera lucida.

Figs. 1-13. *Cleidodiscus mirabilis* Mueller, 1937. 1, 3, Dorsal anchors. 2, 4, 5, Ventral anchors. 6, 7, 8, 9, 10, 11, Accessory pieces. 12, 13, Ventral bars.

Figs. 14-29. *Urocleidus torquatus* n. sp. 14, 17, Ventral anchors. 15, 16, Dorsal anchors. 18, 22, Dorsal bars. 19, 20, 21, Ventral bars. 23, 24, Cirri. 25, 26, Accessory pieces. 27, 28, 29, Hooks.

Figs. 30-46. *Urocleidus variabilis* n. sp. 30, 33, Dorsal anchors. 31, 32, Ventral anchors. 34, 37, 39, Dorsal bars. 35, 36, 38, Ventral bars. 40, 41, Cirri. 42, 43, Accessory pieces. 44, 45, 46, Hooks.

Figs. 47-53. *Urocleidus grandis* Mizelle and Seamster, 1939. 47, Dorsal anchor. 48, Ventral anchor. 49, Dorsal bar. 50, 51, Ventral bars. 52, Accessory piece. 53, Cirrus.

Figs. 54-63. *Urocleidus chaenobryttus* Mizelle and Seamster, 1939. 54, Accessory piece. 55, Cirrus. 56, Ventral anchor. 57, Dorsal anchor. 58, 59, Ventral bars. 60, 61, 62, Dorsal bars. 63, Hook.

PLATE 1

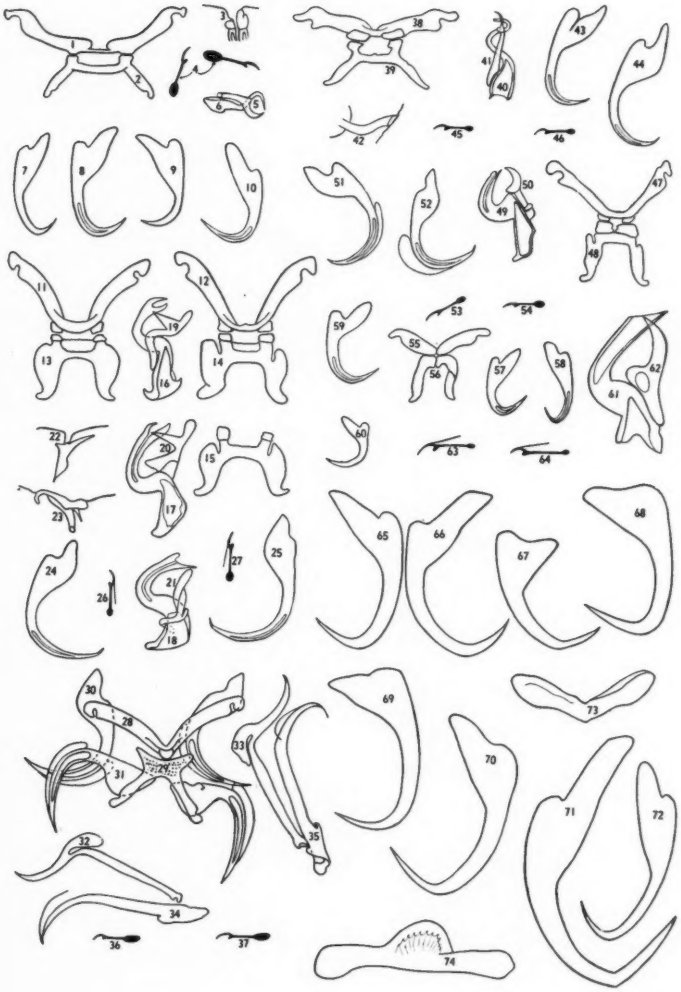
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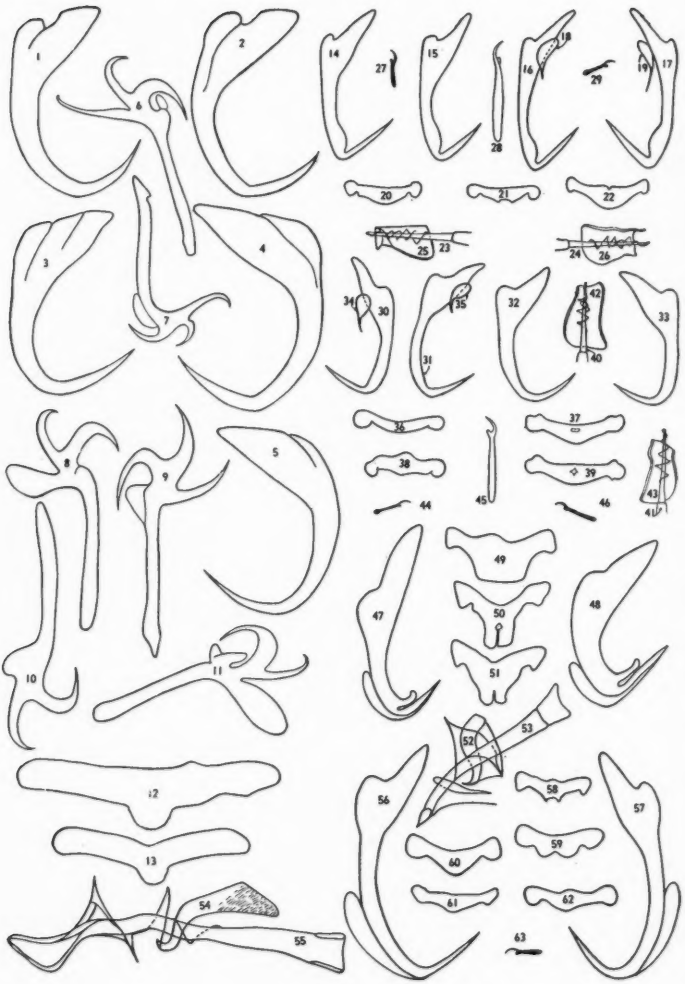
PLATE 2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An Index to the Opinions Rendered by the International Commission on Zoological Nomenclature*

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The International Commission on Zoological Nomenclature was constituted by the Third International Zoological Congress convened in Leyden, Holland, in 1895. This Commission was established in response to the growing realization of need for stabilization of interpretation in the numerous problems of zoological nomenclature upon which different individuals and groups were sadly lacking in agreement. Though organized in 1895, the Commission in its final form was reconstituted in 1898 with a membership augmented to 15 commissioners. Its prime function was that of studying the diverse codes and practices then extant among systematists and from these to formulate a series of definite principles for the guidance in interpreting earlier works and in directing the future of zoological nomenclature. This immediate interest led to the formulation of the International Rules of Zoological Nomenclature which were adopted in 1901, at the Berlin Congress. The most generally available edition of these rules for English speaking zoologists is that published in 1926, in the Proceedings of the Biological Society of Washington (Vol. 29, pages 75-104). As finally prepared, this code differentiates between rules and recommendations. Many items were under consideration which either the Commission or the Congress did not deem worthy of recognition as fixed rules and these are inserted as recommendations for the guidance of all workers.

In fields as highly specialized as those of taxonomy and nomenclature, individual opinions and biases greatly influence individual practices. Persons of varied cultural, educational, and political backgrounds cannot agree on the relative importance of the numerous problems that they confront in science any more than they can agree on all matters of politics, government and religion. It is only natural, therefore, that the rules, which represent the combined judgment and the compromise of a truly representative international congress, stress only those broad general principles upon which almost universal agreement is possible. For this and for varied other reasons many controversial matters were never brought to a point of agreement that would permit of incorporating final decisions of these matters into the body of the rules. In spite of the incompleteness and indefiniteness of the rules, they have well served as the backbone of an attempt at world wide agreement in a plan for stabilizing zoological nomenclature. Behind the rules and the recommendations the approval of fellow zoologists and the desire to avoid their disapproval exercise a controlling influence over the workers in the profession

* A Contribution from the Zoological Laboratory of the University of Illinois.

favoring the support of the findings of the Commission, for neither the Commission nor the Congress possesses any power for enforcement of regulations.

Some time prior to the Boston Congress (1907), some zoologists began to request the Commission to pass judgment on matters of interpretation of the code. Out of this request grew the functions of sitting as a tribunal to hand down decisions on disputed points. These decisions expressed as Opinions and the body of evidence gathered in reviewing the cases comprise the body of material for which the present index has been prepared. The commissioners gave consideration to problems of interpretation of the code and to the extension of the general principles to specific instances upon which individual opinions and interpretations might differ. In this capacity the Commission sat in judicial consideration of specific instances of conflicting evidences, in cases where application of the rules was not clearly evident and in others where no provision under the code was available for guidance. Requests for consideration originated from any interested person or group upon whom then devolved the obligation of preparing the background of each case for submission to the Commission. All references and all interpretations were then reviewed critically by the Commission. In this connection the former secretary of the Commission, the late Dr. Charles Wardell Stiles, has rendered an immeasurable service to all future generations of zoologists in the patient yet ardent zeal with which he attacked the problems of involved and intricate interpretations for his colleagues. Meetings of the Commission were held in conjunction with the International Congresses and between Congresses much of the work was carried on by correspondence. Opinions and reactions of representative leaders in the various fields were sought, especially in controversial cases where the judgment involved principles outside the realm of simple application of rules or practices already established. Upon the completion of the study of a case, a committee formulated an "Opinion" on which a vote of the commissioners was taken. Then if the opinion prevailed it was reported to the next Congress where a favorable action culminated in publication of the official opinion on the specific instance under consideration. Such opinions have extended value in application to similar cases and therefore the worker in taxonomy and its nomenclature has immediate need for the consideration of all expressions of judgment by the Commission even though they may pertain to entirely different groups from the ones in which he is individually interested.

In 1907, the Commission published in Science (Vol. 26:522-523) Opinions 1 to 5 which had been reported to the recently convened Boston Congress. The Smithsonian Institution, in 1910, agreed to "distribute the printed Opinions to 1,100 libraries, to the members of the International Zoological Congress and to a limited list of specialists." To this end, Opinions 1 to 5 were reprinted by the Smithsonian Institution along with additional opinions that had accumulated. In July, 1910, a 61 page pamphlet designated as Publication 1938 was issued containing opinions 1 to 25. Since that date the Smithsonian issued at irregular intervals 7 other pamphlets for current opin-

ions, each appearing as a separate publication, not in any of the regular series of volumes, but with continuous pagination. Dates and inclusions of these pamphlets are shown in the following table:

Opinions 1-25 (Publ. 1938) July, 1910	Opinions 52-56 (Publ. 2169) May, 1913
Opinions 26-29 (Publ. 1989) Oct., 1910	Opinions 27-65 (Publ. 2256) March, 1914
Opinions 30-37 (Publ. 2013) July, 1911	Opinion 66 (Pub. 2359) Feb., 1915
Opinions 38-51 (Publ. 2060) Feb., 1912	Opinion 67 (Publ. 2409) April, 1916.

Thereafter, for a considerable period of time, the World War disrupted the continuation of all international cooperation and the definite programs of the Commission and its sponsoring International Congress were suspended. When international considerations again became feasible, the Commission became active. In 1922 the Smithsonian Institution resumed publication of the Opinions but in the meantime a decision had been reached whereby they were to be allocated in the series designated as the Smithsonian Miscellaneous Collections and, to this end, volume 73 of that series has been reserved for the opinions so that beginning with Opinion 68 they all appear in the same volume. Part 1 of Vol. 73 (Opinions 68-77) was issued on January 31, 1922. To date, 8 parts of this volume have appeared, the most recent one (Part 8) including Opinions 124-133, was published on October 28, 1936. Unfortunately, a second World War, with the disruption of scientific programs and cessation of all constructive efforts at international cooperation has again imposed a restraint upon all progress of the Commission. Under these circumstances, further concerted advances in nomenclature seem indefinitely blocked. In the meantime, volume 73 of the Smithsonian Miscellaneous Collections remains incomplete and therefore no index to the opinions is available. A brief summary of the first 90 opinions is included in the edition of the International Rules published by the Biological Society of Washington (19926, pages 91-103). Similarly, many textbooks dealing with problems of zoological nomenclature have summarized some of the opinions but the original documents contain so very many pertinent discussions of the problems that the serious student of nomenclature finds the summaries of about as limited value as abstracts are to the research worker. The original must be consulted before one may catch the full significance of the article.

The 133 opinions already published have far greater significance than that which pertains to the individual cases with which they deal. In the aggregate, they represent guide posts of professional opinion on allied problems and as such they constitute an essential complement to the rules, highly comparable to the records of cases supplementing the text of the law in the legal profession. To the majority of workers in nomenclature, these opinions and rulings are like a library without a catalog and lacking any sequential arrangement. Even knowing that a given item is there, it can be located only by hunting for it. A number of years ago the present writer prepared an analytical index to the opinions for his personal use and for the convenience of research workers in his laboratory. The preliminary index thus prepared included only the major problems on which action had been taken. A series of successive

combings of the text of the opinions has greatly expanded the original index. Several workers, including the late Dr. Charles Wardell Stiles, have expressed the belief that a compilation of this sort would be welcomed by all zoologists who deal with problems in taxonomy.

Presumably on the completion of Volume 73 of the Smithsonian Miscellaneous Collections, an official index will be prepared. In the meantime, the present compilation may serve the workers more satisfactorily than the available alternative procedures of reading through or thumbing through the 133 opinions to locate a point in question. Dr. C. G. Abbott, Secretary of the Smithsonian Institution, has kindly consented to the publication of this material.

After each entry in the index, the one or more numerals are to the individual opinions in which the name or the item is mentioned. In many instances, an opinion and its discussion extend through a large number of pages and therefore the reader will be required to do some hunting before he locates the exact reference within the opinion cited. This might have been avoided by insertion of page numbers for each reference but it seemed that this would unduly burden the index without commensurate return. This is particularly true, since after opinion 67 there is no consecutive pagination, each separately published part carrying independent page numbering.

As a presumably final act in the review of the evidence regarding the availability of a generic name under the code, the Commission from time to time has published in the opinions "Official Lists of Generic Names." The first of these official lists of generic names was included in Opinion 66. The names here included had been approved by a special committee appointed by the Commission and had been published in Science and in the Zoologischer Anzeiger, as well as in the Proceedings of the Ninth International Zoological Congress. Under existing circumstances, though the official lists of generic names are not absolute, the names that have been admitted are relatively well assured of permanence in nomenclature. In consequence, the present index gives recognition to the officially recognized generic names by placing in this index after the name, in italics, the number of that opinion in which the name was admitted to the official list.

In entering references to principles, no consistent attempt has been directed to the inclusion of all instances under each heading, for in many cases the commissioners were divided on the classification of the point in question. One group of commissioners might consider the spelling of a generic term as a "lapsus" while another group might with equal sincerity be able to find no evidence to support such a classification.

Authors' names, in so far as they constitute only the authority for a generic or specific name, have been omitted in this index. On the contrary, if an author is cited and his work is discussed as part of the evidence advanced in formulating the opinion, then his name is included in the index as a significant entry. The shading in degree between simple citation as authority for a name

and the discussion of taxonomic principles makes it impossible to apply an absolutely uniform practice in treating the names of authors in an index.

The publication of an index seems particularly fitting at this time because two factors are definitely operating against further continuation of the operations of the International Commission on Zoological Nomenclature. The first of these, the global war, already has been mentioned. The second offers just as effective a block to resumption of international consideration of problems after the close of the war, namely, an unfortunate factional split which has threatened the whole basis for stabilizing nomenclature. At the Berlin meetings (1901) a rule was adopted which provided that no amendment to the code should thereafter be presented to any session of the Congress for vote unless the amendment had been in the hands of the Commission for at least a year prior to the meeting of the Congress. This provision has seemed extremely important to many American zoologists as a safeguard against hurried, emotional enactments under pressure, sponsored and colored by local and possibly unrepresentative interests. Unstudied action arising immediately from the floor of the Congress might readily disrupt all the established bases for permanent solution of the problems of nomenclature. Under powerful and impulsive leadership even as essential a rule as the law of priority might be deleted from the code for there have always been some who could see in it only the disrupting effects of familiar names being supplanted by less familiar prior names. Such individuals fail to see beyond the slight temporary personal inconvenience to the goal of ultimate stability through application of priority.

At the Padua meetings (1930) serious differences of long standing broke out anew. In the face of this internal dissension there is room for serious doubt if a Congress dominated by local groups capable of bringing radical changes to immediate vote can continue in any program of stabilizing zoological nomenclature.

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Corollary and Commentary for "Climate and Evolution"

Karl P. Schmidt

In its principal outlines, the history of the study of animal geography has been a simple one. The mass of geographic data on the distribution of animals, accumulating from the time of Linnaeus and before, could not be integrated or interpreted while the doctrine of special creation was current. Once a belief in evolution gained acceptance, animal and plant geography became of great interest in any broad review of biological problems, in the description of the host of new forms being discovered, and in any general account of the life of the world as a whole.

Darwin devoted two chapters in the *Origin of Species* to this subject, which was seized upon by Wallace for amplification into a separate treatise, resulting in his two-volume *Geographic Distribution of Animals,* in 1876. This work clearly forms the classical foundation of animal geography as a distinct branch of zoology. While great improvements in the classification of animals and great advances in our knowledge of their distribution have now reduced the importance of Wallace's large volumes to an historical one, the somewhat ponderous major work was fortunately followed by a much more readable book, addressed to a wider audience, under the title *Island Life.* Published in 1880 and revised by Wallace himself in 1891, this remains an extremely useful and interesting introduction to the general subject.

A general stability of the continents in their major outlines, i.e., to the borders of the continental shelf, now at a depth of about 200 meters, was regarded as axiomatic by Darwin and Wallace. The shallow seas at Bering Strait, suggesting past connection between Asia and North America, the similar shallows with obviously unstable island connections in the East Indies, extending via New Guinea to Australia, and the existing isthmus of Panama were regarded as the only connections between continents that require consideration for an understanding of the distributions of terrestrial life.

Subsequent to this classical period, a school of zoogeographers arose whose members "created continents as easily as a cook makes pancakes," as Darwin had remarked about the speculators of an earlier era who had postulated vast interchanges of land and sea to account for the distribution of groups of plants and animals found on more than one continent. To the new school, connections between all of the continents of the southern hemisphere in low or high latitudes in early geologic periods and various trans-Atlantic and trans-Pacific continental "land-bridges" of later date were thought to account for the distribution of groups of animals now confined to the southern hemisphere. Thus the marsupials now living in Australia and South America were thought to

require a direct past land-connection to explain this distribution. The aglossal frogs and the burrowing amphisbaenid lizards, mostly confined to South America and Africa, were similarly regarded as indicating a South Atlantic land bridge. Speculation as to such direct continental connections, and as to past connection of the various southern continents with each other via Antarctica, became commonplace. A few critical objections, like those of Handlirsch in 1913, were lost in the general rush of specialists, each accounting for the dispersal of his group of animals by a new hypothetical land bridge of his own. A geological basis for such zoological land bridge hypotheses was provided by a group of geologists not averse to land-bridge speculations of their own. The hypothesis of a paleozoic "Gondwana Land," extending from Australia and India across the Indian Ocean area to Africa and across the existing south Atlantic to South America was based by the German geologist Neumayr on the wide range of the Permian fern *Glossopteris,* and in the distribution of marine fossils that outline the Permian seas. This opened the way for other paleogeographic speculations, like those of Suess and Haug, and these in turn to a whole school of land-bridge zoogeographers, including Hutton, Forbes, von Ihering, Arldt, Osborn, and Scharff.

A new phase in the study of animal geography was inaugurated by an essay by W. D. Matthew entitled *Climate and Evolution,* published in 1915. This constitutes a cogent argument for return to more critical and more logical thought in studies of animal distribution, and especially for an integration of the evidence from living animals with that from the fossil remains of extinct forms. Matthew boldly rejects most of the land-bridge hypotheses for the dispersal of mammals during Tertiary time, and marshalls the evidence from paleontology against all such connections except that between Asia and North America via Alaska, and the Panamanian bridge between North and South America. Modern studies of animal geography are characterized principally by the efforts of Matthew and a few disciples to make themselves heard against the more popular land-bridge building group. Matthew's essay failed to attract the attention it deserved, partly on account of its publication during the world war then in progress; but it afforded a model and a set of guiding principles to a group of students under Matthew's influence in the American Museum of Natural History in the decade after its publication. It was soon out of print; it is pleasant to record its republication by the New York Academy of Sciences in 1939 as a handsome separate volume.

The main theses of *Climate and Evolution* rest on a broad view of animal life as seen on the vast perspective of cycles of erosion and uplift in geologic time; on the geological principle of isostasy; and on the theory, supported by specific evidence, that the main theaters of evolution of animal life have been the larger land-masses of the northern hemisphere. The occurrence of primitive forms in a given region had come to be regarded as an important criterion of a center of origin, following especially C. C. Adams. Matthew shows that this is essentially fallacious reasoning; evolution with natural selection would usually crowd the more primitive ancestral types (when they do not become extinct) *out* of the areas of origin of the more advanced derived forms, and into

peripheral regions; and the data from Tertiary mammalian fossils is marshalled to prove this principle. The accumulation of primitive and otherwise relict forms of life in the continents of the southern hemisphere is shown to be due to such long-continued radiating dispersal from the nearly continuous land masses of the north, North America and Eurasia, constituting the "Holarctica" of animal geography, in which the more advanced and modern types have replaced the earlier ancestral forms. Australia, South America, and the southern half of Africa project southward from the northern continents like great peninsulas, and as the more primitive forms enter them at the north, they have necessarily accumulated in these peninsulas from successive waves of dispersal, and of evolution.

A great number of forms of reptiles and amphibians present this pattern of dispersal, sometimes with isolated relict forms like *Sphenodon* in New Zealand (which may be thought to represent an early Mesozoic outpost of Australasia) or the duckbill in Australia and Tasmania; sometimes with groups found in all three of the southern continents like Leptodactylid frogs, primitive geckos or side-necked turtles; and frequently with groups confined to one or another pair of the three southern continents. The tree frogs of the family Hylidae in Australia and South America, the amphisbaenian lizards in South America and Africa and the geckos of the genus *Diplodactylus* in southern Africa and Australia illustrate such transverse faunal relations in the southern hemisphere. It is the presence of the primitive types in the southern hemisphere that is interpreted according to the Matthewsian principles as relicts of southward dispersal from the northern hemisphere, while they are thought by the "Bridge-builders" to necessitate land connections at various ages from South America to Australia, from Africa to South America, and from Australia to Africa, or even of all the southern continents together, via Antarctica. The whole system of land connections proves to be fallacious when the faunas of the southern continents are reviewed in toto, for each region exhibits so peculiar a fauna that the problems raised by a land bridge hypothesis are frequently much greater than those it is proposed to solve.

In so far as the Tertiary and the general pattern of the dispersal of the essentially Tertiary Mammalia is concerned, Matthew's review of the evidence from both recent and fossil forms is conclusive, and is supported by the further evidence accumulated during the subsequent twenty-five years. Using the clear picture of Tertiary dispersals thus derived as a principle, Matthew applies it in turn to the more Mesozoic and Paleozoic times, in which the paleontological evidence is necessarily less abundant and less clear. As it becomes steadily more evident that the dispersals on which the larger outlines of the distribution of living reptiles is based are essentially Mesozoic, such a principle becomes more and more essential in the complex maze of the distribution of groups originating in successive periods. Transverse faunal relations between Africa and South America in different groups may arise in different ages, and the impossibility of a land connection in the Tertiary does not *ipso facto* preclude pre-Tertiary land connections. Thus the relation between the aglossal frogs *Xenopus* and *Hymenochirus* in Africa and *Pipa* and *Protopipa* in South

America may be a very ancient one; Noble's argument in the *Biology of the Amphibia* is thus not valid on this point. The reason for the interpretation of the Mesozoic relations in the light of the Tertiary conditions is a logical one; it is the interpretation of the more remote and more obscure in the light of the nearer and better documented. It is the application of "Law of Parsimony," to prefer the simpler explanation to the more complex.[1]

I find in conference with my paleontological colleagues that they tend to stress the correlation of the large scale radiating dispersal of animals from Holarctica with parallel pulsations of climatic change, spreading in widening circles from the same center. This is in part implied in Matthew's theses. My colleagues believe that the changes in Holarctica through a long term cycle from desert to steppe and to forest or through the same series in reverse has led to evolutionary changes in the animals of the Holarctic centers. They believe further that the displacement of the more primitive ancestral forms has been into outlying or concentric regions, in which, by a time lag in the secular climatic change, these same forms found a natural refuge. Whether or not this is the primary process of dispersal set forth by Matthew, other large scale factors are implicit in *Climate and Evolution*. The peneplanation of the continents seem often to have been world wide, as have been periods of mountain building. Widespread uniformity of climate would facilitate and promote dispersal to the ends and fringes of the continents. It is evident, however, that evolution must continue even *during* periods of uniformity and within uniform environments. In this event the accelerated evolution on the larger land masses, with its resulting biotic pressure, will tend (among other effects) to drive the ancestral and less well adapted forms to the periphery. The more varied faunae with their larger populations exhibit a superiority over the less varied and smaller; this is somewhat analogous to the principle of mass action in chemical reactions. Actually, the superiority in question appears to be produced by a greater variety of selection pressures in the more varied environment; and it must be noted that the superiority is often one of intangible characteristics, i.e., of physiology or of behavior. If there is such a general superiority of Holarctic animals and plants, biotic pressure on those of the peripheral regions is a direct result even in the absence of secular climatic change. The crux of the argument lies in evolutionary superiority of the forms of life in the larger Holarctic land masses, not in the question of successive secular climatic changes.

The general thesis of superiority and hence of evolutionary advancement of both the plants and the animals of the northern hemisphere is documented by the history of introductions in various parts of the world. Almost any weed or insect pest that can be named proves to have come from Europe or from Eurasia. The history of the brown rat is a striking case in point. A most readable volume, Thomson's *Naturalization of Plants and Animals in New Zealand* provides vivid illustrations. It is most instructive that the superiority

[1] Well stated by Ernst Mach in his address on "The economic nature of investigation in Physics" (1882).

demonstrated is quite as much one of herbivore over herbivore as of predatory animals, and that it extends to insects and even earthworms. The familiar North American weeds and insect pests, together with the house mouse and the black and brown rats among mammals, and the house sparrow and starling among birds, exhibit the usual superiority of Eurasian forms over those of the smaller segments of the northern hemisphere. Our North American forms are quite as much at an advantage in South America and Australia, and we have even provided a few counter pests to Europe, such as the muskrat in central Europe and the potato beetle, introduced in the south of France in the last world war and since extending its range year by year. The superiority of the Eurasian races to isolated native races elsewhere is pitifully clear in the extermination of the Tasmanians, the decimation of the South Sea Islanders by the white man's diseases, and in the relict populations of kinky haired blacks in the Malayan Islands. Though perhaps to be read with some reservation (according to my anthropological colleagues) Griffith Taylor's essay on this subject is illuminating and clearly an expansion of Matthew's brief section on this topic (1936, pp. 40-45).

Southern Animals not Represented in the North

There are a few groups of animals with representatives in Africa and South America that have been especially cited as evidence of land connection across the South Atlantic. These include especially the aglossal frogs, the amphisbaenas and leptotyphlopid blind snakes, and the rich fresh-water fish faunae of characins and cat-fishes. The most cogent evidence *contra* Matthew in this respect is that from certain families of mussels and fresh water snails in the recent faunae of these two continents, since fossil evidence of these forms is wanting in the northern hemisphere, and would be expected from the abundance of fossils of other groups of mollusks. This evidence is well presented by Pilsbry and Bequaert (1927, p. 598-601), who point out, however, that the evidence from the non-appearance of the groups in question in the north is negative evidence. It must be pointed out further that the classical 'hedge' regarding such evidence, the imperfection of the paleontological record, remains a necessary and valid consideration even after the great advances in paleontology in the last two generations. The *weight* of evidence remains against a transverse connection of Africa even in the Mesozoic. The discovery of dicynodont reptiles in Eastern Turkestan and New Mexico is a striking example of the radical changes still to be expected in our knowledge of the distribution of extinct creatures.

In the case of the fishes, the possibility of entrance into the fresh-water habitat from the ocean must be considered. It will be remembered that the distribution of *Galaxias*, long thought to indicate juxtaposition of the southern continents, is now interpreted as having been trans-oceanic, since some of its forms have been shown to be catadromous.

The Argument in a Circle

The mass of zoogeographic literature by the 'land-bridge school,' by mere inertia, has led to persistence of theories of connections between the southern continents after their foundations had been destroyed by *Climate and Evolution* in 1915. The whole theory of continental drift rests with one foot on the supposed *zoological* necessity for some such connections, while attempting to comply with the requirements of the geological evidence of isostasy, which makes it impossible to assume the elevation of great areas of the ocean floor. Thus Wegener cites a whole list of paleontological and biological arguments in Chapter five of *The Origin of Continents and Oceans* with no clue to the fact that Matthew had demolished this whole argument in so far as it refers to the Tertiary, and that this evidence for the process of dispersal in the Tertiary throws grave doubt on land-bridge reasoning as applied to earlier periods.[2]

Similar citation of defunct land-bridge theories is exhibited by Hobbs in *Earth Evolution and its Facial Expression,* who writes of the theory of the permanence of ocean basins as having been found to be "hopelessly in opposition to later discoveries in faunal geography," six years after the date of *Climate and Evolution.* Even worse is Bailey Willis' *Isthmian Links,* in which the theory of broad land bridges is rejected on sound geological grounds, while fantastically improbable narrow isthmuses are maintained across the South Atlantic and Indian Oceans on account of the supposed requirements of zoological data. It may be mentioned that the Lemurian land bridge from India to Madagascar, which still appears in Willis' maps, had been shown to be thoroughly contrary to zoological evidence by Fritz Sarasin in 1910, i.e., even before Matthew.

Zoogeographers who favor land-bridge speculation in their turn cite the geologists who have rested their arguments on those of zoogeographers, until it seems all but impossible to escape from such whirlpools of circular reasoning.

Relict Forms on Islands

Oceanic islands, which have received their animal and plant life by more or less 'accidental' dispersal, have a heterogeneous fauna, as has been conclusively set forth by R. C. L. Perkins in his review of the origin of the Hawaiian fauna (1913). Controversy has arisen over the oceanic nature of the Galapagos Islands because certain elements of their fauna are strikingly archaic. I believe that such primitive elements in the fauna of islands may well reflect the age of their first colonization. Much of the hazard accompanying an accidental landing of an individual animal is absent when the landing is on an uninhabited shore. As the island becomes progressively more populated, the difficulty attending the establishment of any new entrant increases sharply. Thus an

2 A most convincing argument against continental drift is offered by Jeffreys (1924), who shows by impressive mathematical analysis that the centrifugal force within the earth is by far the most powerful that could act on "floating" elements of the crust, so that the continents, if they move at all, would aggregate at the equator.

archaic cast in an insular fauna may indicate something of the age of the island in question, but does not contraindicate its oceanic origin. With the more intelligent evaluation of the agency of storms in populating islands (cf. especially Darlington, 1938) much that has appeared in print regarding the origin of the West Indian fauna appears clearly as nonsense (cf. especially Scharff, 1911, p. 274). Most of the vertebrate fauna appears to be plainly an archaic one, and some relations with the Galapagos may be discerned (as in the lizards of the genus *Cyclura*). Such relations point to a common origin of the faunae as to date and source, and obviously not to land connection between the Antilles and the Galapagos.

I have elsewhere called attention to what I believe to be an important factor in the isolation of birds on islands (Schmidt, 1930, p. 287), namely their homing instinct, which reenforces isolation and counteracts their power of dispersal by flight.

Secondary Centers of Evolution

While in the larger outlines of dispersal according to Matthew it is customary to speak or write of "southward dispersal from Holarctic centers," it is implicit in *Climate and Evolution* that this is a *radiating* dispersal, and that the relict forms are *peripheral*. It is evident that for many centers of evolution on a smaller scale some of the peripheral forms may be at the east or west or north as well as at the south, and that some such cases will present apparent exceptions to the over-all picture of the main outline of animal distribution. A well-known example of radiating northward dispersal appears in Ruthven's interpretation of the dispersal of the garter snake genus *Thamnophis*. The northward dispersals of this group appear to be essentially postglacial, after a period of being crowded southward by the advance of the continental ice.

In my paper on the Lower Californian reptilian fauna in 1922 I pointed out the interesting evidence for long-continued radiating dispersal of lizards and snakes from the Colorado Desert. Since 1922 the discovery of *Xantusia arizonae* and *Uta sleveni* has contributed important evidence in support of dispersal from this desert region as a center.

Still within the North American continent, the Appalachians afford an example of a secondary center of dispersal for the most advanced of the families of salamanders, the Plethodontidae. Even these are represented in Europe, and as in the case of the newts and hell-benders, their primary dispersal must have long antedated their more specifically American diversification into genera and species.

On a much greater scale is the northward irruption of the autochthonous South American fauna at the time of re-establishment of the Panamanian connection in the Pliocene. The ability of such ponderous primitive creatures as the ground sloths and glyptodonts to emigrate in the face of the more advanced North American fauna must be interpreted as due to their great specialization, as well as to their great size. Their early extinction in the north

may have been because of continued biotic pressure, as their extinction in the southern continent appears to have been also.

Hanging Relicts

Another series of animal groups that offers exceptions to the rule of accumulation of relict forms in the southern continents is presented by what may well be termed 'hanging relicts.' The family Ascaphidae, for example, is regarded as the most primitive living group of frogs, with the convincingly primitive character of vestigial tail muscles demonstrated by the late G. K. Noble. In this family, the New Zealand frogs of the genus *Liopelma* are thus exactly as peripheral as should be expected from the premise of radiating dispersal from Holarctica. But the other genus, *Ascaphus*, the tailed frogs of western North America, though they accord with the belief that the group as a whole was of northern origin, have remained in the north instead of being forced to emigrate to South America. Thus *Ascaphus* is a hanging relict. The most probable explanation that occurs to me for the failure of this frog to emigrate to the southern continent lies in its extreme adjustment to the special niche of the torrential mountain stream, with its ice-cold waters. The tropics might well afford an insuperable barrier to such a cold-adapted form, and at the same time, its adjustment to the mountain torrent (especially evident in the sucker mouth tadpole) removes it from the direct competition of the more advanced frog families.

The lemurs of the African forest (the "bush-baby" and its relatives) seem similarly to be out of step with the retirement of the lemur group into the southern tips of the Asiatic peninsulas and into Madagascar. The inadmissibility of a "Lemurian" land bridge has been mentioned above, and is of course contra-indicated by the pottos and galagos. What explains their presence in the midst of the highly developed (and essentially Holarctic) African fauna? These creatures are extraordinarily adapted and restricted to nocturnal habits, and are thus removed to a significant degree from the competition of the mainly diurnal monkeys. It is noteworthy that the Madagascan lemurs include actively diurnal forms.

The whole group of salamanders, plainly an ancient one, is almost confined to Eurasia and North America, entering the tropics with only a few forms (and these specialized rather than primitive). This may well be the largest taxonomic group (an order) to be considered as a "hanging relict." The explanation of cold adaptation early in the phylogenetic history of the group may be advanced with reasonable assurance for the salamanders.

The common opossum is a conspicuous hanging relict, apparently preserved by secretive and nocturnal habits, together with great tenacity of life and great fecundity, in the North American theatre of mammalian evolution. Unlike the ground sloths, glyptodonts, armadillos, and porcupines, which entered North America from the south, the opossum appears to have persisted on our continent throughout the Tertiary. The earliest known fossil remains, little different from the modern animal, are from the Cretaceous of Wyoming.

Peninsular Life

The three great southern continents are thus in a sense peninsulas extending southward from the land masses of Eurasia and North America, whose essential similarities of both plant and animal life justifies their union under the biotic concept of Holarctica. The common faunal characteristics of the major peninsulas is their accumulation of peculiar forms of life, frequently primitive, and frequently with surprising *transverse* relations.

What is the case with the numerous southward projecting peninsulas of Europe, Asia, and North America? Should not these, on a smaller scale, repeat the faunal characteristics of the southern continents? Here is the acute observation of William Thiselton-Dyer (in 1909, long before *Climate and Evolution*): "The extraordinary congestion in species of the peninsulas of the Old World points to the long-continued action of a migration southward. Each is in fact a cul-de-sac into which they have poured and from which there is no escape."

Thiselton-Dyer's observation applies to the Spanish, Italian, and Grecian peninsulas with their Mediterranean faunas, many elements of which are relicts of the relatively recent southward compression of animal and plant life by the advance of the ice. The Iberian peninsula, for example, has six genera of amphibians and nine of reptiles not represented in Central Europe. Several of these are wide-spread Mediterranean forms; but the amphisbaenid lizard *Blanus* reappears only in Asia Minor. This group of lizards must have spread from an ancient center, here interpreted as probably somewhere in Central Europe.

Much more conspicuous and more obviously ancient accumulations of relict forms are exhibited by the Indian and Malayan peninsulas. The fauna of Ceylon (which represents that of the tip of the Indian peninsula) was analyzed by Fritz Sarasin in 1910 (as cited above). He demonstrated some four successive waves of invasion from the north, with residual elements from all of them left in the modern fauna. Though now in need of revision, Sarasin's lists of the amphibians and reptiles of Ceylon and South India exhibit a wealth of peculiar forms, of which such remarkable creatures as the shield tailed snakes are endemic, while notably distinct genera like *Draco* (the flying lizard) *Trimeresurus* and *Agkistrodon* (pit vipers), and the fresh-water turtle *Geoemyda* are characteristically present in Malaya and the south Indian region, while absent in the major part of the Indian peninsula. This distribution is paralleled by various birds and mammals, notably by the lemurs.

In North America, I have myself analyzed the reptilian fauna of the Lower Californian peninsula from the standpoint of successive waves of invasion from the north and of accumulation of relicts at the tip of the peninsula (1922, pp. 611- 629). At the other side of the continent, the Floridan peninsula exhibits a fauna that is essentially an appendage of the rich and distinctive life of the southeastern United States. This great fauna and flora as a whole is plainly a relict of the Cretaceous and early Tertiary world wide biota in the

northern hemisphere, as is shown by its relations with the animals and plants of eastern Asia. The reptiles of the Floridian peninsula include several distinct genera, such as the amphisbaenid lizard *Rhineura,* the peculiar scincid lizard *Neoseps,* and the remarkably elongate snake *Stilosoma.* In addition to these generic endemics, there is a whole series of subspecies characteristic of Florida. These are more obviously and recently derived from the Southeastern fauna; and several of these, in turn, have given rise to slightly modified subspecies at the southern tip of the peninsula. Considering that the origin of the Floridian land area is certainly much more recent than that of the Lower Californian peninsula, the Floridian fauna is characteristically peninsular.

"Paleopeninsulae" or "Fossil Peninsulas"

Few paleogeographic changes in the connection of the continents are so well established and dated as the interruption of the Panamanian isthmus between North and South America, which interruption must have continued from the Eocene to some period in the Pliocene. It is evident also that there must have been a connection between the Atlantic and Pacific at the Isthmus of Tehuantepec at one or more periods. Thus there was a great southern peninsula from the main area of North America for long periods of time, extending to Costa Rica at some periods and to the border of the Mexican Plateau at others. This peninsula was broad based, like India, and outward dispersal from the main mass of the continent would inevitably force wave after wave of faunal elements into it. It is interesting to enquire as to whether some traces of an accumulation of relict forms can be detected in Central America and in Mexico. That this is the case is immediately attested by the taxonomic diversity of the fauna. Among the reptiles alone, there are twenty-four families represented between Panama and southern Mexico, not counting the soft-shelled turtles, the Trionychidae, and the land turtles proper, the Testudinidae, which enter northern Mexico. This compares with twenty-two families for the whole of the vastly larger and topographically more varied South American continent. Even this disparity is not the measure of the relative richness of the two regions, for no less than nine of the South American families are quite clearly late entrants into the southern continent from the north; the net relation is 24 families in Central America and only 14 characteristic of South America. It does not appear that any of these ancient South American groups, all but three of which are now present in Central America, have made any extensive reinvasion of the northern continent. Thus the Central American families include twelve that belong to the Mesozoic fauna of North America that originally invaded South America; and twelve that accumulated in this area while it was a Tertiary peninsula from the northern continent. The families of reptiles here considered are listed in the accompanying table. It will be seen that the West Indian fauna includes 13 families, of which only three belong to the Tertiary group; but the remaining ten families may be thought of as derived from Central America rather than a "South American Element" in the West Indies.

The four well-defined families of reptiles, now confined to Central America,

and thus specifically characteristic of the Central American "Paleopeninsula," are the Dermatemydidae, a group of turtles abundant in North America throughout the Tertiary; the Helodermatidae, the beaded lizards, now evidently relicts, with only a single American genus with two sharply defined species, one of which is found in southwestern Mexico (with another genus in Borneo); the Xenosauridae, another family with only two species of a single genus, in southern Mexico and Guatemala; and the scincoid, burrowing Anelytropsidae, which have been thought to be related to some of the African burrowing lizards, but have certainly been long isolated.

The families of amphibians and reptiles suspected of being Pliocene entrants to South America are the Plethodontidae, Bufonidae (*s. s.*), Ranidae, Chelydridae, Kinosternidae, Emydidae, Testudinidae, Crocodylidae, Achrochordidae, and Crotalidae.

Thus the four families that failed to enter South America after the elevation of the Isthmus of Panama present a class of hanging relict whose adjustment to local conditions or whose phyletic decline and consequent want of dispersal pressure explains their geographic position; while their correlation with a paleopeninsula has provided the setting for their evolution and brings them into accord with the peripheral distribution of older forms in general.

The origin of the tropical components of the herpetological fauna of the Americas was discussed, essentially on the lines here set forth, by E. R. Dunn in his acute analysis of this fauna in 1931. His essay is fundamental to further discussion of the origin of Central American fauna, and it is hoped that he will review and amplify it in the major work on the amphibians and reptiles of Lower Central America on which he has long been engaged. Since the date of his paper, no evidence has been brought forth to contradict his analysis of the fauna in general into a modern Holarctic element, an older element, the "Old Northern," and the "South American." I have had the good fortune to be able to contribute to the knowledge of the northern origin of one of the conspicuous elements in the South American fauna, in tracing the turtle genus *Podocnemis* to the North American Cretaceous (Schmidt, 1940).

The interchanges between the mammalian faunae after reestablishment of the Panama bridge were so rapid and so extensive that the examination of mammalian evidence for the Central American paleopeninsula will depend upon studies of Central American paleontology yet to be made. Paleontologists are well aware of the problems offered in this region (Olson and McGrew, 1941). By inference from the data available, there was a great accumulation of Tertiary forms in Central America, already extinct farther north, at the time of elevation of the Panama bridge.

The Mexican Plateau, outlined by the tropical lowlands, is ecologically a peninsula from the American desert and grass-land region. A remarkable series of species of snakes, each obviously the most primitive in its genus, characterizes this region. These forms are *Storeria storerioides*, which has the loreal shield present and thus links *Storeria* proper with the ancestral colubrid form; *Pituophis deppei*, which has undivided prefrontals, and this differs from the

familiar species of the United States; and *Diadophis dugesii*, which Blanchard regards as the most primitive living member of its genus. To these may be added another parallel case pointed out by Dunn, *Salvadora pulchra* of Central America and southern Mexico, in which the enlargement of the rostral, otherwise characteristic of this genus, is not developed. These several annectant forms, with others among the rattlesnakes that may belong with them, obviously fit the Matthewsian principle of peripheral dispersal of ancestral forms; they as plainly indicate that the origin of these forms and of the groups they represent was *not* on the Mexican Plateau, but in a Tertiary center of evolution to the north. The outward emigration of the ancestral members of the group may be obscured by the postglacial repercussion, with rapid northward spread of many forms into unoccupied territory ; but it remains the major factor in the dispersal pattern of families and genera.

TABLE 1.—Families of Reptiles in the American Fauna

Family	Central America	West Indies	South America	
			Early Invasion	Late Invasion
Chelydridae	×	0	..	×
Kinosternidae	×	0	..	×
Dermatemydidae	×	0	0	0
Emydidae	×	×	..	×
Testudinidae	only at the north	0	..	×
Trionychidae	only at the north	0	0	0
Pelomedusidae	0	0	×	..
Chelidae	0	0	×	..
Alligatoridae	×	0	×	..
Crocodylidae	×	×	..	×
Gekkonidae	×	×	×	..
Iguanidae	×	×	×	..
Xenosauridae	×	0	0	0
Anguidae	×	×	..	×
Helodermatidae	×	0	0	0
Teiidae	×	×	×	..
Amphisbaenidae	×	×	×	..
Scincidae	×	×	..	×
Anelytropsidae	×	0	0	0
Boidae	×	×	×	..
Leptotyphlopidae	×	×	×	..
Typhlopidae	×	×	×	..
Anilidae	0	0	×	..
Achrochordidae	×	0	..	×
Colubridae	×	×	×	..
Amblycephalidae	×	0	×	..
Boigidae	×	×	×	..
Elapidae	×	0	×	..
Crotalidae	×	0	..	×

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Work with Vertebrate Animals on the Hastings Natural History Reservation

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Opportunity came, in 1937, to the Museum of Vertebrate Zoology of the University of California, to undertake a kind of museum work new for it and to extend the scope of its program by establishing a field station. Here, many of the procedures and ideas resulting from the previous thirty years of its development might be applied and tested more intensively and possibly more effectively than by the conventional methods of exploration in the field. Without in any way relaxing the pursuit of studies already in progress over a larger area, it was desirable to concentrate on the development of a continuous record of biotic changes on some restricted sample of ground.

The provision of the site and other essential facilities for such an enterprise resulted from the decision of Mrs. Russell P. Hastings to offer her 1600-acre ranch in Monterey County to the University of California for this specified use. Her aim was to initiate a program that would make the area serve some really useful purpose in educational or scientific ways. Mr. and Mrs. Hastings proposed not to rid themselves of the land and the responsibilities of its management, but to take an active part in the development and maintenance of the venture. This involved supplying funds for the regular expenses as well as for special items. Also their active interest has led them to participate in the solution of problems which arise constantly.

When the Hastings Reservation was established, in the fall of 1937, the declared purposes were (1) to preserve an area in California's coastal region where native plants and animals may live undisturbed by human use of the land, and (2) to provide for continuous study of vertebrate animals, especially their numbers and relationships to their surroundings, as these relationships change in the annual cycle and from year to year. The two major objectives remain as outlined in the beginning. This short account has been prepared to define briefly the nature of the Reservation and of the study being conducted. The material included may be of special interest to persons who have had some part in the undertaking or who contemplate taking a share in it. Description of procedure and explanation of results must be presented in a more expanded form.

Because people always have been more or less intimately aware of the animals and plants that surround them, it is easy for them to assume that the lives and manners of all these living things are well known. A person is therefore likely to be surprised when he discovers how little actually is known concerning these topics. The direct, economic value of this knowledge for people may be easily overemphasized, but it is not likely that the value of

knowing more about the affairs of the living world will be too highly considered. The nature of the problem and its significance have been recognized by a few students of wild game, in particular by Professor Leopold when he indicated that the highest value of wildlife research lies not in enhanced game crops but in enhanced understanding of natural mechanisms. More game benefits only a few; more comprehension raises the cultural level of all. W. P. Taylor, repeatedly, has stressed the point that invisible bonds link organic life in a thousand intimate ways with its physical and chemical surroundings, so that what we really have is a single great system including minerals, soils, waters, vegetation, animal life, and atmosphere. Thus the wildlife problem is one of land use just as much as is the forest problem, or the farm problem, or the grazing problem.

Observation and study on the Reservation are being conducted on the assumption that they will be continued for many years, or at least for long enough to repeat the full cycles of the longer-lived organisms present there. At the same time special effort is made to keep the results of the study so organized that loss of effort would be at a minimum if the whole undertaking were to be discontinued. This involves the assembly of facts and materials so that they go as directly as possible into a scheme of interpretation of the biology of the area. Numerous types of graphic and tabular summaries and analyses are maintained and extended as the information becomes available. Much time has gone into working out plans for the assimilation of newly gathered items into the growing analysis with a minimum of clerical work.

The analysis of the biota of a small, restricted area is too complicated to be carried out by a single worker. But it must be carried on as a single study if suitable progress is expected. While the single study may be best guided by one person, it is necessary to combine the energies of many persons having many traits and capabilities to obtain the essential facts. The tendency, currently practiced, for each person or small group of persons to study some single restricted topic in field natural history may produce interesting results, but the desired understanding of them must come from co-ordinated and harmonious application of the efforts of many workers. Competition may provide incentive for increased activity, but it should not be permitted to interfere with the progress of other workers.

It is obvious that many persons working with the common objective of interpreting the life on a small area can accomplish more than an equal number of isolated individuals, provided efforts are supplementary rather than duplicating or disconnected. The present study is being built around the notion that the combined efforts of many persons are required to make even a gross interpretation of the biological events on so small an area as the Hastings Reservation.

In practice, observers on the Reservation include volunteers who have special interest in the work here and paid workers who spend varying lengths of time at this special exercise to supplement training available at the University. In less than six years forty persons have been so employed on the Reser-

vation for a total of more than 4800 working days, or more than equivalent to one full-time observer for fifteen years. This represents approximately 50,000 hours of work in the field, and it has produced 25,000 full pages of field notes. Thirty of these persons are now enrolled, or have been recently, in advanced biological courses at Berkeley. In a cooperative program of field study, where many persons contribute and where some of them begin with little special training for that particular type of work, it is desirable to adopt many uniform procedures and at the same time to maintain opportunity for inventiveness in as much as possible of the work. Prospective naturalists may thus greatly reduce the expense and amount of time ordinarily required in the apprentice stage. They also at the same time contribute importantly to the fund of materials here being assembled.

Additional to the work of this group has been the volunteer help of eighty-five persons who studied and identified specimens and other material sent away from the Reservation. The materials preserved in the permanent collection are mainly insects and other invertebrate animals and plants including the lower groups. These specimens are used in our study of food habits of the vertebrates. Also a knowledge of them helps us to understand the local distribution and other responses to the environment of these larger animals. There are indications, too, that this kind of collecting is worth while for the new information it produces concerning these lower organisms and their occurrence. Many species have been described or redescribed from specimens obtained on the Reservation.

The need for the best available authority in determination of our working collections is readily apparent. Repeated need arises, however, to convince the expert that materials returned by him to the Reservation will be safely preserved and that they will serve some useful purpose there. The collection and preservation in proper manner of special groups of organisms is a difficult procedure and the results sometimes try the patience of the specialist. But the kind of study undertaken requires an adequate reference collection authentically identified, and we are anxious to supply material to qualified persons willing to examine it and report back along with the return of identified specimens.

An important element in the conduct of a study of this kind is the availability of suitable equipment and materials for making, recording, and storing the results of observations. We found the Reservation already well stocked with buildings, tools, and numerous other items required for continuous work there. An appreciable amount of time, however, is needed to select and assemble such additional apparatus as traps, microscopes, telescopes, field glasses, cameras, and weather recording instruments. These and the building now available for safe storage of them and of the records, as well as for improved working quarters, provide incentive for study.

Location is important in determining the fauna and flora at any site. The Hastings Reservation is especially well suited for exhaustive study because its location provides isolation from disturbance and comparatively easy access to towns for supplies. The place is easy to find on a map (see Fig. 1). It is two

and one-half miles east of the old site of Jamesburg, formerly a post office, in northern Monterey County, California. Other well-known landmarks are on the Monterey Peninsula, twenty-five miles to the northwest, containing Monterey, Pacific Grove, and Carmel. Salinas is nearly the same distance

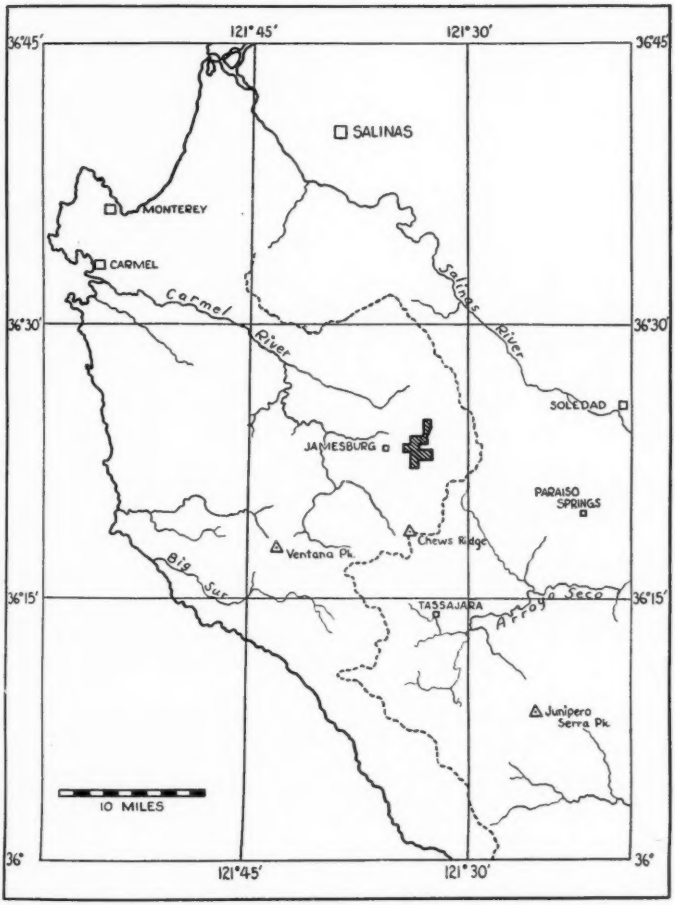

Fig. 1. Map of the northern part of the Santa Lucia Mountains, in Monterey County, California, showing the location of the Hastings Reservation, near Jamesburg. Broken line indicates the divide between drainage directly into the Pacific Ocean and that into the Salinas River.

away and also toward the north. It is less than twenty miles to the Pacific Ocean on the west, being close to twenty to Point Sur and about twenty-five to Point Lobos which is eight miles north and twenty-four miles west of the Reservation.

Northern Monterey County is almost exactly halfway along the coastal border of California and is approximately one-third the way, from south to north, along the Pacific side of the United States. Although the proximity of the ocean brings few animals to the Reservation, its influence in modifying the climate is important. In this connection it is instructive to compare this site with Point Lobos and to study the great contrast in living things at the two closely adjacent places.

The Reservation contains parts of sections 4, 8, 9, 16, and 17, T 18 S, R 4 E, M.D.M., Jamesburg Quadrangle, Monterey County. The lines 36° 23′ N lat. and 121° 33′ W long. meet on the Reservation not far from the headquarters where observations have been most concentrated. Following each of these lines away from this spot helps to locate it with respect to other places on the earth's surface. Northward, the line passes near Lassen Peak and Tule Lake, in California, Mount Rainier, in Washington, and just to the west of Great Bear Lake in the far north. Toward the east the latitude passing through the Reservation comes near or passes through the following places: Owens Lake, California, the Grand Canyon, Arizona, Norfolk, Virginia, Gibraltar, Algiers, and Tokyo.

Possible significance in knowing these localities on the same longitude is concerned with long movements and migrations of the animals. The recently emphasized importance of change in day length in the activities of animals depends upon latitude. Comparison of the annual programs of activity of animals at various places in the same belt of latitude helps to evaluate this factor in relation to other possible factors. The effects of increase or decrease in day length should be equal everywhere along this line. Deviations in the annual program of breeding activity or migration would then be caused largely by other factors, even though the program is determined to some extent by the timing effects of day length.

The site lies on the upper border of an area of grassland at the north end of the Santa Lucia Mountains, being included in the drainage of the Carmel River though not in the immediate vicinity of that stream. Altitudinally, the Reservation extends from about 1500 feet up to around 2750 feet. It includes some woodland which intermingles with and grades into chaparral. (See Figs. 2 to 7.) Shreve, in early studies of the range, divided the vegetation of the Santa Lucia region into four communities: Hygrophytic Forest, Mesophytic Forest, Chaparral, and Grassland. The two types of forest are not always clearly distinguishable, but the first, characterized by redwood and tan oak, is limited to lower parts of the canyons, within twelve miles of the coast and does not reach the Reservation. Chaparral, characterized by predominance of shrubs with broad sclerophyllous leaves, occupies the greatest area in these mountains.

Fig. 2. A view across the Hastings Reservation and toward the north shows the grass-covered hills with patches of chamise on the southward exposures.

Fig. 3. A near view of an open grass-covered hill interspersed with chaparral and scattered oaks.

The two main types of chaparral represented on the Reservation, however, are lacking in broad-leaved sclerophyllous shrubs.

The conspicuous plants of the vicinity, including several species of evergreen and deciduous oaks, the madrone, buckeye, and numerous tall shrubs besides the chamise, occur in western North America where the summer precipitation is less than one-fifth of the total, and predominantly where the total precipitation is between 10 and 30 inches and where temperature extremes are moderate.

The herbarium of flowering plants and ferns collected and maintained on the area consists of 1500 mounted specimens representing approximately 550 kinds. A separate set of seeds representing most of the species has been assembled, and effort has been made to collect as many as possible of the lower plants and animals found associated with them. Attention has been given especially to the fungi, lichens, liverworts, and mosses, and among animals to the arthropods. As yet, however, no adequate study has been made of the vegetation as revealed by community studies.

Climatologically, proximity to the sea is a potent basic condition affecting the area. This stabilizes the temperature in the vicinity, increases the rainfall, tempers the aridity of the summer with a blanket of fog, and reduces the evaporation, at the same time that it reduces the total number of hours of sunshine and increases the total wind movement. Although this fog blanket rarely reaches so far inland as the Reservation, its effect on the weather there is distinct. Much of the ground is well protected by high ridges from the high wind.

In the past five years the temperature at the Reservation has been below freezing only a few times and it has reached 100° only rarely. The precipitation, which is nearly all in the form of rain and which comes mainly in the months from December to March, averages around 22 inches. In the last five seasons it has ranged from a little below sixteen inches to a little more than forty-one inches. These conditions favor the activity of animals and of observers throughout the year.

A soil survey of the Reservation was completed in November 1941 by the Division of Soils, University of California. In the course of the survey eleven different soil series were recognized and sixteen soil types were mapped. These soil types were combined with variations in slope and degree of erosion to make a total of forty-eight different separations. The dominant soil type of each series was sampled and analyzed. The resulting maps and preserved sample specimens provide important aids to the working out of better understanding of the relations of mammals and other vertebrate animals to the soil.

Expressed in a single sentence, the program followed is to assemble the story of the natural biotic productivity on the Reservation as completely as information warrants, and to continue the gathering of material as the equipment permits. A starting point in this problem is the definition of populations of organisms. This means much more than determination of numbers, but validity of ideas as to numbers determines the soundness of further interpretation. The aim is not merely to reach a total of individuals, but rather to

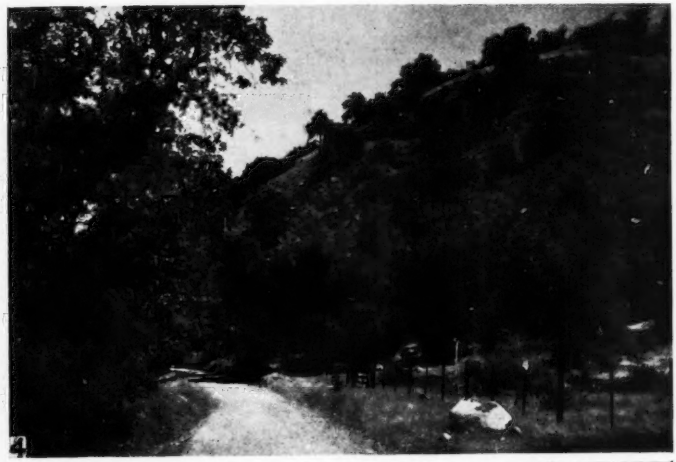

Fig. 4. On some steep canyon sides, rising steeply from a stream, the transition from moist to very dry situations comes in a short distance.

Fig. 5. Dry woodlands where blue oaks are conspicuous cover the gentle slopes near the tops of the hills.

trace the deviations in numbers through space and time and to understand what causes these deviations. Population is a convenient term for this kind of knowledge.

As to birds, in an area where special difficulties interfere with any attempt to count actual numbers, additional means must be used to learn something of their populations. Certain characteristics of the birds, which may be thought of as properties which help to indicate their populations, are useful to study as a substitute for actual measurements. It is possible, too, that these properties provide better definitions of populations than would the counts alone. For each kind of bird occurring on the Hastings Reservation this phase of the study involves definition and tabulation of at least fifteen kinds of these properties, as follows: Name, seasonal status, months present, nesting season, song season, daily activity, habitat, abundance, density, dominance, frequency, sociability, vitality, stratification, and biological constants.

For the 137 kinds of birds known to inhabit the Hastings Reservation a classification as to seasonal status shows 50 residents, 22 summer residents, 26 winter visitants, 15 transients, and 24 of casual occurrence. As to degree of vigor (vitality), revealed by ability to complete the life cycle, 37 are accidental, 53 have incomplete, and 47 show complete life cycles on the Reservation. Total number of species for each month shows remarkable uniformity through the year with a peak in April and lesser ones in September and November. The month with fewest kinds is June. This is not to be accounted for by lack of searching, for more days (632) have been spent in the field in June than in any other month, and these were longer days than at other times of the year. Number of species for each month is as follows: January 81, February 88, March 95, April 104, May 94, June 78, July 80, August 85, September 93, October 83, November 89, December 82.

Computation of the index for frequency of observation, a ratio of days a species is observed to the number of days spent in the field, is especially useful in comparing changes in populations from year to year as well as in making comparisons with other regions. Seventeen, or 12 per cent, of the 137 species have been recorded on more than 80 per cent of the days; 81 or 60 per cent have been seen on fewer than 20 per cent of the days. These figures are based on 650 days of recording over a 3-year period.

The constants are primary characters which vary little from place to place, and we can make use of determinations made elsewhere in the range of the species. Most of the properties listed, however, are so variable as to require study and description on each spot of land. The biological constants chosen as significant for this analysis are weight, wing length, tail length, number of eggs in set, egg length and breadth, sex which broods, egg-laying interval, start of incubation, incubation period, and time spent by young in nest.

When all these items have been assembled for each species, we should have a fairly sound foundation from which to speak of the population of birds in the area and of their place in the biota. Many of them are sufficiently flexible

and variable that much evidence is needed for the determinations. But evidence short of completion will have some degree of usefulness. Already a high proportion of the items has been obtained for our area.

The notion has been stressed that work on the Reservation is carried out on the supposition that working out the individual life histories of the species is the most profitable way to study the whole biotic community. As further indication of how this applies in practice, it may be useful to summarize briefly the amount and kind of attention so far given to the more prominent kinds of birds. In place of some satisfactory measure of this attention, counts of the filled pages of notes must serve. Thirty-seven, or 27 per cent of the kinds of birds have, to date, received special attention. These are listed with indication of the amount of evidence assembled and a comment on the nature of the observation.

Study of Prominent Birds on the Hastings Reservation

Species	Pages of notes	Nature of study
Cooper Hawk	534	at 2 nests with young
Sparrow Hawk	163	a week watching young in a nest
California Quail	229	year round
Mourning Dove	151	11 days at 2 nests-incubation
Barn Owl	32	analysis of 3500 food items
Black-chinned Hummingbird	90	a week at nests with young
Anna Hummingbird	131	4 days-nest building, incubation
Red-shafted Flicker	211	10 days at nest with young
California Woodpecker	264	20 days at nests, 20 days at roost
Nuttall Woodpecker	111	9 days at nests with young
Say Phoebe	128	foraging and roosting behavior
Western Flycatcher	181	14 days at 2 nests
Wood Pewee	299	20 days at nests
Cliff Swallow	233	3 weeks at 2 nests
Yellow-billed Magpie	362	year round, except detailed nesting
Crow	305	16 days at 1 nest, and year round
Plain Titmouse	138	year round
Wren-tit	243	22 days at nests—eggs and young
California Thrasher	120	3 days incubation
Western Bluebird	285	20 days at one nest
Blue-gray Gnatcatcher	291	11 days at nests
Loggerhead Shrike	209	winter behavior of single bird
Hutton Vireo	177	136 hours at 1 nest
Solitary Vireo	122	10 days at nests
Warbling Vireo	81	9 days at nests
Orange-crowned Warbler	62	7 days at a nest
Tolmie Warbler	67	5 days at a nest
Bullock Oriole	359	275 hours—2 nests at once
Black-headed Grosbeak	87	6 days at nests
Lazuli Bunting	402	35 days at nests
Linnet	144	3 days at a nest, and year round
Green-backed Goldfinch	161	10 days at nests
Lawrence Goldfinch	233	20 days at nests
Brown Towhee	92	2 days at a nest
Spotted Towhee	187	9 days at nests
Junco	125	5 days at 1 nest
Song Sparrow	120	11 days at a nest
37 species	6920 pages	

Mammals provide an important part of the life on the area despite the fact that they are so retiring in the light and generally so inconspicuous as to be seldom seen in the daytime. The few diurnal species may be studied by the usual procedure of cruising until an example is encountered or by setting up permanent or temporary blinds as watching stations. Evidence as to numbers and material for the study of adaptive structure and internal parasites come from traps set in staked quadrats or in unmeasured lines usually placed outside

Fig. 6. A section of the canyon where most of the field observations are being made. The long field to the right of the center is the area live-trapped for mammals over a four-year period.

Fig. 7. Streamside vegetation at the base of a north-facing, shaded slope. The moisture and variety of vegetation here favor a high population of animals.

the Reservation boundaries. For more detailed and prolonged studies of populations we have established surveyed tracts where only live-trapping is conducted and where effort is made to preserve the normal habitat as well as the normal population of animals as a part of the study.

The principal one of these areas was established in July, 1938, and trapped as continuously as facilities permitted through the subsequent four years. Previously this had been a creekside field containing approximately thirteen acres regularly planted to oats. (See Figs. 6 and 7.) The long, narrow strip extends down a canyon for about 2200 feet. Mammals were trapped mainly among the trees and bushes on the border. However, as the vegetation became established in the years after termination of cultivation, mammals extended their ranges out across the open ground. The evidence obtained here pertains to many segments of the problem of populations as well as to the life histories of the separate kinds of mammals. Of the thirty-four mammal species known on the Reservation, nineteen have been trapped in this small strip of land, and in numbers indicated by the following tabulation.

Kind of Mammal	Number marked
Didelphys virginiana	8
Sorex ornatus	47
Mustela frenata	3
Spilogale gracilis	1
Citellus beecheyi	246
Eutamias merriami	24
Thomomys bottae	3
Perognathus californicus	570
Dipodomys venustus	4
Reithrodontomys megalotis	230
Peromyscus californicus	307
Peromyscus maniculatus	603
Peromyscus boylii	123
Peromyscus truei	66
Neotoma fuscipes	351
Microtus californicus	1047
Mus musculus	6
Sylvilagus audubonii	61
Sylvilagus bachmani	39
Total	3739

These numbers are of individuals trapped, marked, and released. In no instance do they represent actual numbers present, but they give a minimum that has some value in estimating the true population. If this area represents an average for the whole Reservation, which may be a justifiable assumption, then the mammal population for the whole area could have been no less than half a million individuals in the four-year period. This gives some notion of the vast numbers of organisms available for study on one small bit of ground. It is easy, also, to imagine how great an influence must be exerted by all these animals upon their surroundings and the other kinds of organisms occupying the land with them.

The place of these items in the whole study may be indicated by a statement covering all the included activities at the Reservation. The provision of the unique facilities available makes possible the concerted application of numerous devices which reveal simultaneously the happenings of biotic significance. Allotment of energy at present goes to six distinct though related kinds of study selected as a minimum for the program anticipated in 1937. These concern phases of vertebrate natural history, as follows.

Identification of the set of animals and plants normally present. Although still far from complete, this basic set of facts, along with the records of weather and other physical elements, has become sufficient to guide more particular studies. Expanded, this leads to determination in significant detail of occurrence of each species in space and time within the area.

Concentrated analysis of the life histories of selected, important species. This involves detailed written record of long sessions of watching individual animals or groups of animals and reveals adaptations and responses to particular conditions existing here. It thus helps to indicate importance of each species in the whole community.

Population studies of a few kinds of birds especially suited to banding and repeated capture. Applied to winter-visitant species this method reflects influences far outside the Reservation. Thus, we are reminded that life on any area depends on the life and conditions at many other localities. Not even a small unit is self contained and independent.

Marking of small mammals and their subsequent capture. These records show unsuspected relations between species and between the animals and their surroundings. The annual cycle of change in numbers needs to be traced repeatedly if we expect to recognize even the main factors which influence them.

Continuous watching the same animals and plants. This produces an intimate acquaintance with food habits, changes in them through the seasons and from year to year, and their significance for the populations. Identified reference collections are essential for understanding this network of relationships.

Parasites: collection of specimens and analysis of occurrence. Even though not usually conspicuous, they seem sometimes to affect animal populations significantly. Our collections are almost complete enough to permit continuous study of this phase of the whole topic. Here, again, the help of numerous experts enables us to proceed with sound preparation.

In a study of the nature of the land and its inhabitants on a sample area we may direct special attention to some particular group of organisms, even so restricted as birds or mammals. This leads us immediately, however, to consider the single individual as representing the group and the relation between it and the atmosphere and soil about it as well as between it and other living things. No choice remains but to become familiar with all these elements in order to understand any one of them. The familiarity cannot be a superficial kind, nor can it be too minutely exhaustive if we are to progress. The proper balance of attention to the possible topics must be established and modified continuously to be effective. A suitable plan of work for a day may require a complete change at any hour. Thus we prepare to meet the continuously shifting problem with a continuously shifting attack, but we expect by this devious procedure to contribute something of value toward the final synthetic interpretation of what happens on the land.

Experiences on the Reservation point to several preliminary conclusions of special interest. Preservation and protection of natural conditions on wildland, even where buffered by land not intensively used, require continuous and alert vigilance to minimize disturbance from outside agencies; casual guarding is insufficient. Abundance and variety of living things present on small bits of normally suitable land are greater than is generally recognized, even by experienced biologists. Rapidity and intensity of environmental changes and the responses to them by living things are more clearly discerned with close attention; thus it becomes necessary to give more and more thorough attention to these phenomena. Sound conclusions concerning relationships observed, it has developed, depend on making specific identifications of organisms involved, a procedure not generally practiced, or even possible, in ordinary field work in natural history. The facilities provided by Mrs. Hastings are proving to have a special value, not at first anticipated, for the way they can be used by prospective naturalists to supplement training available at the University.

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Book Reviews

THE OCEANS. By H. U. Sverdrup, Martin W. Johnson and Richard H. Fleming. Prentice-Hall, Inc., New York, 1942. x + 1087 pp. 265 figs and 7 charts. $10.00.

OCEANOGRAPHY FOR METEOROLOGISTS. By H. U. Sverdrup. Prentice-Hall, Inc., New York, 1942. xv + 246 pp. 69 figs. and 4 charts. $4.65.

Oceans and their attendant seas cover 71 per cent of the earth's surface and provide 300 times as much habitable space as lands and fresh waters combined. They have produced the gerat bulk of fossils and sediments from which life's history is reconstructed and from which its past habitats are inferred. They exert profound influence upon the distribution and activities of modern organisms as well as upon the climates of both hydrosphere and land.

These relationships indicate the importance of oceanography to the biologic and geologic sciences and to meteorology. The need for a modern and comprehensive treatise on the subject is shown by the fact that a quarter century has passed since Schokalsky's book appeared and thirty-one years since Murray and Hjort published *The Depths of the Ocean*. During that time new instruments have been devised, new techniques of interpretation perfected, and a vast amount of information secured. Much of it is not available to workers in institutions whose libraries do not specialize in oceanography.

The Oceans summarizes this progress, often in surprising detail. Its 1087 closely printed pages begin with a general survey and progress through such subjects as bottom topography, physical and chemical properties of sea water, density and the marine "heat budget," and dynamics of ocean currents. One chapter deals with vessels, instruments and methods of collecting. Geologists will be specially interested in chapters on waves and tides, water masses and currents, and one on marine sedimentation. The last of these contains a thoroughly up-to-date survey which should serve the advanced teacher as well as the research worker in stratigraphy, sedimentation or paleoecology.

Organisms receive seven of the twenty chapters. The first of these deals with chemical characteristics of marine life in relationship to salt water. It is followed by a chapter on the seas' population which perhaps is the least satisfactory one in the book, since it presents little more than a simple classification of marine organisms. More satisfactory, and much more stimulating, are discussions of the relationship of phytoplankton and marine animals to the physico-chemical properties of their environment. The chapter on interrelationships of organisms stresses food chains, movements and concentration, as well as the role of bacteria. In such a comprehensive book there apparently was not room for a treatment of marine societies, which is unfortunate. There is need for a summary and analysis of social complexes, especially in temperate seas. Generalizations about them (not always correct) figure largely as a basis of inference in paleoecology.

Each chapter is followed by an adequate though not an extensive bibliography.

As its title indicates, *Oceanography for Meteorologists* is designed to provide the student of weather and climate with information about the seas' affects upon our atmosphere. It therefore discusses such topics as physical properties of sea water (currents, salinity, temperature, eddy viscosity, conductivity, etc.), the heat regime of salt waters, ocean currents, waves and wind currents, and water masses. The heat regime ("budget" again is Sverdrup's term) is specially well developed. It treats the effects of radiation to and from the ocean, the exchange of heat between atmosphere and sea and evaporation with its geographic, annual and diurnal variations. Currents also are described in considerable detail. The only bibliography is a list of eleven general works at the end of the preface.

It is evident that in content this book closely parallels several chapters in *The Oceans* without duplicating them, since objectives and emphasis are distinct. For libraries that

need or can afford only one volume, the larger is the most serviceable choice. Those workers whose interest is limited to weather or climate will find the smaller book adequate and thoroughly useful.—CARROLL LANE FENTON.

EXTINCT AND VANISHING MAMMALS OF THE WESTERN HEMISPHERE WITH THE MARINE SPECIES OF ALL THE OCEANS. By Glover M. Allen. Special Publ. Amer. Committee Int. Wild Life Prot., No. 11, xv + 620, figs. $4.50.

A tragic and romantic interest attaches to the extinction of conspicuous or remarkable animals within the time of historic records, especially when such extinctions are brought about by the greed and callousness of man. The present work is not only valuable to zoologists but is an interesting and readable account of an important topic for the non-professional conservationist. A survey of the kinds of animals in danger of extinction, together with the lessons to be derived from an account of actual extinctions, forms an indispensable basis for conservation policies and projects. We are thus extremely fortunate to have Dr. Allen's competent account of these mammals of the western hemisphere and of the marine mammals of the world that are declining in numbers or in any danger of extinction, the more so as it is the last comprehensive work completed before his untimely death. Allen interprets the limits of his list broadly so that interesting West Indian and South American forms whose extinction took place in pre-Columbian times are included.

The application of the modern classification of mammals into their geographic subspecies to the list of forms in danger of extinction adds greatly to the technical importance of the present work, and of course adds numerous completely extinct forms to the list, like the eastern bison or eastern mountain lion. For the most part this adds important material to the book; but the fact that the grizzly bears are still divided into 76 named forms is a considerable disgrace to mammalogical taxonomy. In many of the North American mammals discussed there has been a steady restriction of range, with extermination at the east and north accompanying the increase of the white population. Such restriction of range is especially conspicuous in the case of the wolves, larger cats, the elk, and the bison. There are conspicuous cases of near extinction and return to considerable populations, as in the Plains bison, various races of beaver, the Californian sea elephant and the sea otter.

The modern status of conservation of whales is well set forth, and the treatment of the marine mammals in general is excellent and comprehensive.

It is much to be hoped that the companion volume by Dr. Francis Harper on the mammals of the Old World in this category may be completed and published in comparable format. The work is provided with a useful bibliography and a comprehensive index.—KARL P. SCHMIDT, Field Museum of Natural History.

THE MAMMALS OF EASTERN UNITED STATES. By William J. Hamilton, Jr. Comstock Publishing Co., Inc., Ithaca, New York. 1943. 432 pp., 30 plates, 184 figs. $4.00.

The latest book by W. J. Hamilton deals with all the present day land mammals naturally inhabiting the states east of the Mississippi River. The aim was to give brief descriptions and accounts of distribution and habits. This calls for plates and distributional maps. Another important objective was to impart to the beginner or the indoor worker some of the enthusiasm and enjoyment which keeps the author in search of new discoveries in the field. His special preparation includes travel and collecting in nearly all of these states, but more important has been his long series of intensive first hand studies of mammalian life histories. Two hundred and fifty-three kinds of mammals are treated.

For the person working full time with mammals this reference will provide in convenient form much new information as well as a guide to fuller accounts. Some of the casual taxonomic judgments, such as the one pertaining to skunks (p. 160), will have less ready acceptance, for there is no allusion to the kind of evidence studied. Decisions of this kind are important enough to be supported by facts, though probably in a separate publication.

For the young naturalist adequate descriptions of structure and coloration enable him to identify the mammals he finds. Many items, like measurements, weights, and comparisons would be more clearly and concisely presented in tabulations. A possible improvement would be the reduction of prominence given to subspecies the names of which are printed with the most prominent type in the book. The true interest of nearly every reader is in the species and its habits. Both of these kinds of headings are rather hard to distinguish. These detractions are more than compensated for by the contagious enthusiasm for field study which is reflected prominently in every account. Sometimes, the impression of meager knowledge is stressed more than is necessary. The accounts, however, contain much original information, which is sometimes hard to identify among the compiled materials.

Restriction of treatment to the eastern states is not strictly observed. It does make the book more authentic, for a larger share of it could be taken from the experience of the author. But this precludes reference to much information available only from outside the area though at the same time applicable within it. The obvious remedy would be to expand the book to cover the whole country.

The distribution maps represent a great amount of careful study and provide a major part of the book's usefulness. With them, there is little need to refer to, or to have, the text accounts of range. Illustrations include black and white drawings by E. L. Poole as well as numerous photographs which demonstrate characteristics and attitudes of the species. Also they show the need for more good photographs of mammals. Thirteen pages of selected and classified references to the important literature of mammalogy in eastern United States add appreciably to the usefulness of the book. It is a worthy addition to the Handbooks of American Natural History, edited by Professor A. H. Wright.—JEAN M. LINSDALE.

THE IVORY-BILLED WOODPECKER. By James T. Tanner. Research Report No. 1 of the National Audubon Society, New York. xii + 111 pp., colored frontispiece, 20 pls., 22 figs. $2.50.

For persons who may have been accustomed to think of the National Audubon Society as the organizer of Sunday bird walks and summer camps, or as custodian of remote colonies of showy birds, the establishment of its series of Research Reports will be welcomed. They reveal a new kind of activity aimed to provide solutions of immediate problems as well as historical record of special events in the disappearance of species.

The first number by James T. Tanner may have been too late in showing what acts would save the Ivory-billed Woodpecker, but it preserves interesting and valuable facts and establishes a pattern for other surveys that may be undertaken while there is yet time for effective action. The chief value in these books is in arousing the reader to the stage where he recognizes his share in the benefits of preserving samples of wild things and their surroundings. He is then likely without urging to take a part in whatever action is required.

Many critical elements in the precarious state of this species have been detected and evaluated for the remaining few individuals of this the largest North American woodpecker. Structural fitness to obtain food in a place inaccesssible to other woodpeckers—between the bark and sapwood of recently dead trees—restricts availability to tracts of uncut, mature timber. Forests of this kind in southeastern United States have almost disappeared through lumbering. The birds have been able in the past to travel in pairs for long distances to find adequate supplies, possibly permitting concentration of birds in the last small areas of large trees.

Apparently, this woodpecker has been scarce always within its restricted range. This goes along with a naturally slow rate of replacement, with an average of fewer than three eggs to a set. Also it tends to simplify the immediate problem of preservation, leaving only one avenue for action, the preservation of suitable habitat.

Tanner was fully aware of the magnitude of the task assigned to him and he was able to meet and overcome the handicaps of continuous travel and living in many parts

of the southeastern swamp lands. He was fortunate to start with the guidance and special training for this undertaking gained from Professor Allen at Cornell University.

The Society has presented the report in attractive form, though many readers would prefer a smaller format. Apparently, it has not recognized the obligation or opportunity to get the book read by as many people as possible. Instead of offering such a book for sale at a high price, an obvious move would seem to be the printing of an edition large enough to supply copies to everyone willing to look at it. Proper distribution of these results is more important than the preparation of them.—JEAN M. LINSDALE.

AQUATIC PHYCOMYCETES EXCLUSIVE OF THE SAPROLEGNIACEAE AND PYTHIUM. By Frederick K. Sparrow, Jr. University of Michigan Press, Ann Arbor, 1943. xix + 785 pp., 69 figs., frontispiece, 1 pl. $5.00.

This book has long been needed. As the author notes in his preface, Minden's treatment of the lower Phycomycetes, completed in 1915, marks the end of one epoch in the study of these organisms and the beginning of another. By compiling the work of his predecessors and combining it with the results of his own observations, Minden stimulated the study of aquatic fungi and, in so doing, made it inevitable that the accumulation of new information would be greatly accelerated. Sparrow's service is entirely comparable. He has summarized the widely scattered literature and incorporated the information contained in it with the fruits of his own long and critical studies to produce a work which will be of service not only to the mycologist but to all who are interested in the biological and possible phyletic relationships between these forms and other aquatic organisms.

Of the ten orders of Phycomycetes recognized by the author, seven are primarily aquatic and the Pythiaceae of the Peronosporales is partly so. The interpretation of the term "aquatic" is necessarily elastic, the criterion being that the majority of the members of a group occur in water or in damp soil. This has fortunately permitted the inclusion of the Blastocladiales, the majority of whose species have been isolated from the latter habitat. Because modern monographs of *Pythium* and the Saprolegniaceae are already available in English, the treatment of these groups is brief and generalized, as is that of such specialized parasites on land plants as *Synchytrium* and *Physoderma*. The orders treated in detail are the Chytridiales, divided into the Inoperculatae, with six families, and the Operculatae, with two, occupying well over half the space devoted to taxonomic discussion, followed by the Blastocladiales, Monoblepharidales, Plasmodiophorales, Saprolegniales (exclusive of the Saprolegiaceae), Leptomitales, Lagenidiales, and the few genera of the Peronosporales remaining after the Peronsporaceae and *Pythium* have been deducted. These are arranged in two supra-ordinal series, the Uniflagellatae and the Biflagellatae, with the Hyphochytriaceae placed at the end of the former series as a family of uncertain affinities. The sequence has been made familiar to mycologists in a previous publication by the author. The systematic account of each order is preceded by a general discussion embodying a critical account of the significant features which characterize the group as a whole. Aside from the recognition of a number of genera relatively unfamiliar to mycologists whose major interest is in fungi other than these, the most striking feature of this newer taxonomic treatment is the inclusion of *Olpidiopsis* as the type of a new family in the greatly altered and enlarged order Lagenidiales, here embracing nine genera distributed amongst three families. Since the keys are clear and cross references abundant, no intelligent student will have difficulty in locating a fungus under observation because of this or other changes from older treatments. Considering the scope of the work, the number of new species and new combinations is surprisingly small, the total of both being approximately a dozen. The inclusion of descriptions of numerous doubtful species, concerning which full information is lacking, should invite detailed observation of these species by others who may chance to observe them and result in clarification of their status.

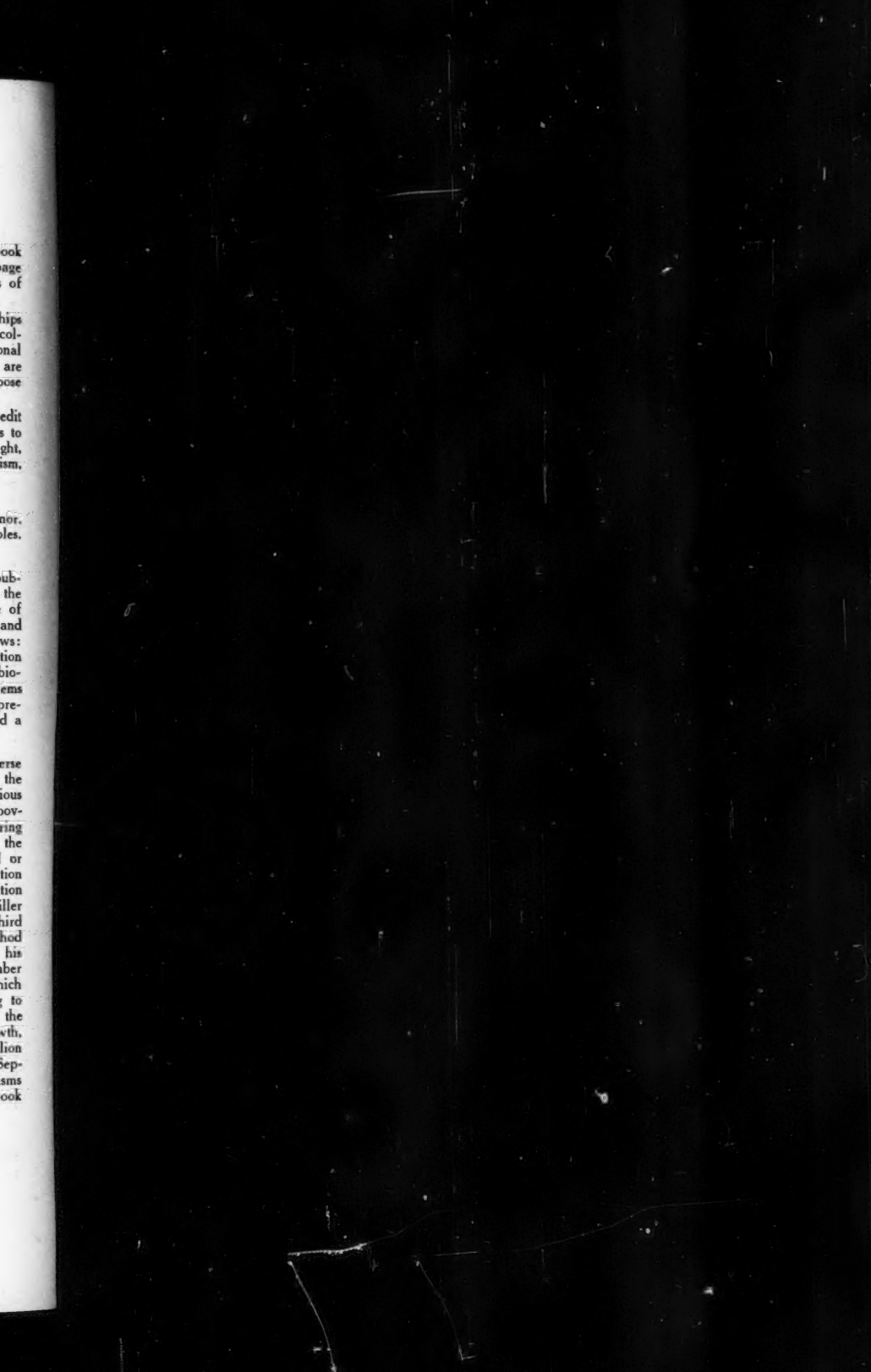
The number of figures is misleading, since most include separate drawings and several represent characteristic genera and species of an entire family or more, the total number of individual drawings, as announced on the wrapper, being 634. A

substantial number of the species recognized are illustrated, and throughout the book references to an illustration are given, not only to the figure, but also to the page where it appears, a practice which may be commended to authors of other books of this sort.

The short introduction includes a discussion of the phylogeny and relationships of the group, notes on their geographic distribution, useful suggestions as to their collection, notes on their isolation and culture and directions for preservation. Additional comments on nearly all these matters occur throughout the text. Forty-four pages are devoted to the bibliography and fourteen to a list of substrata, which serves the purpose of a host index.

The editing has been scrupulously careful and the printing and format are a credit to the publishers. The appearance of this volume should serve as a notable stimulus to the study of these often obscure, but fascinating fungi. Interesting in their own right, increased knowledge of them promises to shed much light on sexuality, parasitism, phylogeny and other problems of general biological significance.—G. W. MARTIN.

WEED CONTROL. By Wilfred W. Robbins, Alden S. Crafts, and Richard N. Raynor. McGraw-Hill Book Co., Inc. New York. 1942. xi + 543 pp., 202 figs., 91 tables. $5.00.

This volume comprises by far the most complete treatise on weed control ever published. The authors have considered both the fundamental and practical aspects of the problem. The material presented should, therefore, be of interest to a wide range of of readers—plant physiologists, horticulturists, landscape gardeners, agronomists and agriculturalists in general. A few examples of the 24 chapter headings are as follows: weeds and human affairs, reproduction of weeds, methods of preventing the introduction and spread of weeds, principles of weed control, tillage methods of weed control, biological control of weeds, the use of chemicals in weed control, special weed problems (three chapters), and special weeds. The subject matter is well organized, clearly presented, and carefully indexed. There is an abundance of excellent illustrations and a wealth of literature cited.

Despite the fact that the book is, in general, highly commendable, a few adverse criticisms are warranted. In a section devoted to the control of weeds by heat, the authors list the advantages of burning without, calling attention at once to a serious disadvantage, namely, the destruction of the organic matter and the resulting impoverishment of the soil. The practice of repeatedly burning the dead debris each spring of the year constitutes such a serious menace to soil conservation in large sections of the country that every effort should be made to discourage it despite certain limited or temporary advantages. A second criticism which this reviewer offers concerns a section on chemical weed control in the chapter entitled, principles of weed control. This section should contain a paragraph in which the properties desirable in a chemical weed killer are listed. Such a list if complete would contain about eighteen items. The third criticism concerns the poor treatment which the authors gave the kerosene spray method for the control of dandelions. Instead of quoting the directions given by Loomis in his most recent publication in which he recommends *one* spray treatment between September 15 and September 30, the authors took their material from older publications (which they cited inadequately) of the Iowa Agricultural Experiment Station. According to these authors, the Iowa Station recommends two applications a year, the first in the spring when the dandelions are reseeding, the second when they start their fall growth, September 1, in Iowa. The writer, having intimate acquaintance with the dandelion eradication program at the Iowa Station, is confident that only one application (September 15-September 30) is now recommended by the Iowa workers. These criticisms are made simply to call attention to certain objectionable features occurring in a book of general excellence.—N. L. NOECKER, University of Notre Dame.